

A model of river benthic algal photosynthesis in response to rapid changes in light¹

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Abstract

A linear relationship has been found between light and community productivity in a river, but the correlation is reduced when radiation varies rapidly due to the passage of cumulus clouds. To investigate the relationship during periods of patchy cloudiness we developed a method of calculating short term variations in oxygen exchange based on oxygen measurements taken at very frequent intervals. The method has a high degree of resolution when used with data recorded at 1-min intervals and the results indicate that large fluctuations in oxygen exchange on time scales of about 5 min can be discerned. Cross-spectral analysis of the productivity data and measured radiation indicated that a linear lead model for algal photosynthesis in rivers is appropriate. This model has the property that the change in net oxygen productivity per unit change in light is enhanced during periods of rapidly varying radiation relative to periods of slowly varying light.

The relationship between primary productivity and solar radiation in aquatic communities has been studied by a variety of methods. Most of the work in standing water communities has indicated that photosynthesis becomes light saturated or inhibited at moderate intensities, but these studies have required containment of the populations and separate productivity estimates at each light intensity. Several investigators have presented data from river communities in which net productivity calculated from free-water measurements of oxygen remained directly proportional to radiation (Duffer and Dorris 1966; Kelly et al. 1974; Hornberger et al. 1976). The light-productivity plots presented by Kelly et al. (1974) and Hornberger et al. (1976) exhibited considerable scatter about a generally linear trend when radiation varied rapidly because of patchy cloudiness.

The deviation from the linear relationship between light and productivity during periods of rapidly varying radiation presented by Hornberger et al. (1976) sug-

gests either that net productivity is not being resolved on a sufficiently fine time scale (and therefore the linear relationship cannot be discerned) or that the direct proportionality model relating light to productivity fails to hold when incident light is not fairly constant. This prompted us to examine the light-productivity relationship using data collected at very frequent intervals to see if the direct proportionality could be recovered or if some other model might be appropriate.

Productivity determination

Data available for analysis consist of digital records of oxygen concentration, temperature, and incident radiation recorded at 15-s intervals on the Mechums River, Virginia. To examine short term variations, we devised an efficient procedure for performing productivity calculations using these sampled data.

If at all given times the longitudinal variation in oxygen concentration along a river segment is negligible with respect to the temporal variation, single-station analysis of diel dissolved oxygen curves is justified (Odum 1956). The oxygen mass balance equation can then be written

$$\frac{dc}{dt} = K(c_s - c) + (P - R), \quad (1)$$

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where c = dissolved oxygen concentration at a fixed point in the stream, c_s = oxygen saturation concentration at that point, K = reaeration coefficient, $(P-R)$ = net community productivity, and t = time. Kelly et al. (1974) have used Eq. 1 with measurements of oxygen concentration and temperature to determine net community productivity by representing $(P-R)$ as a Fourier series and determining coefficients in the series so that the integrated form of the equation provides good predictions of actual measured concentrations. Half-hourly values of oxygen concentrations are used to determine eight Fourier coefficients, and these are sufficient to examine hour-to-hour variation in productivity under smoothly varying light conditions.

A modification of the Fourier series method (which we will call the Fourier transform method) allows calculation of short term (e.g. minute-to-minute) variation in productivity. To do this $(P-R)$ is represented by a Fourier integral,

$$(P-R) = (2\pi)^{-1/2} \int_{-\infty}^{\infty} g(\omega) e^{i\omega t} d\omega, \quad (2)$$

where ω is frequency and $g(\omega)$ is the Fourier transform of $(P-R)$ (see Wiener 1958). Substituting 2 into 1 and integrating from t to $(t + \delta)$ yields

$$c(t+\delta) = e^{-K\delta}c(t) + s(t;\delta) + (2\pi)^{-1/2} \int_{-\infty}^{\infty} \left[\frac{g(\omega)(e^{i\omega\delta} - e^{-K\delta})}{i\omega + K} \cdot e^{i\omega t} \right] d\omega, \quad (3)$$

where for notational convenience

$$s(t;\delta) = \frac{K}{e^{K(t+\delta)}} \int_t^{t+\delta} e^{Kt} c_s(t) dt. \quad (4)$$

The term $s(t;\delta)$ is a time integral of saturation concentration and can be evaluated numerically using temperature data (Kelly et al. 1974). The time interval, δ , can be any integral multiple of the data interval.

The left-hand term of Eq. 3 can be combined with the first two terms on the right-hand side to define a function, $F(t)$, that

can be determined from measured field data. If we let

$$h(\omega) \equiv g(\omega) \left[\frac{e^{i\omega\delta} - e^{-K\delta}}{i\omega + K} \right], \quad (5)$$

Eq. 3 can be written

$$F(t) = (2\pi)^{-1/2} \int_{-\infty}^{\infty} h(\omega) e^{i\omega t} d\omega. \quad (6)$$

That is, $F(t)$ and $h(\omega)$ form a Fourier transform pair (see Wiener 1958). If two continuous functions form a Fourier transform pair, then the sequences obtained from them by discrete sampling are finite Fourier transforms of one another (Cooley et al. 1967). Since $F(t)$ is known from sampled data, $h(\omega)$ may be efficiently calculated using the fast Fourier transform algorithm. Care must be taken to sample at sufficiently small intervals or else considerable error may occur in the estimation of $h(\omega)$ if high frequencies have been aliased (Platt and Denman 1975; Hamming 1973; Cooley et al. 1967).

Once $h(\omega)$ is known, $g(\omega)$ may be obtained easily from Eq. 6. That is,

$$g(\omega) = h(\omega) \left[\frac{(i\omega + K)}{e^{i\omega\delta} - e^{-K\delta}} \right]. \quad (7)$$

Thus, because $g(\omega)$ is the Fourier transform of $(P-R)$, net productivity can be calculated from $g(\omega)$, again using the fast Fourier transform, without loss of temporal resolution beyond that determined by the data interval.

Field and analysis methods

Measurements—Data were obtained from the Mechums River (in Albemarle Co., Va.), which drains a forested and farmed basin on the east edge of the Blue Ridge Mountains. Details of nutrient range and volume flow are given by Kelly et al. (1974). The river bottom is composed of silt, sand, gravel, and a few rocks. The benthic algal community is dominated by diatoms. The macrophyte *Podostemum ceratophyllum* is present on a small proportion of the rocks. A quantitative description of the bottom substrate and algal pigment concentrations

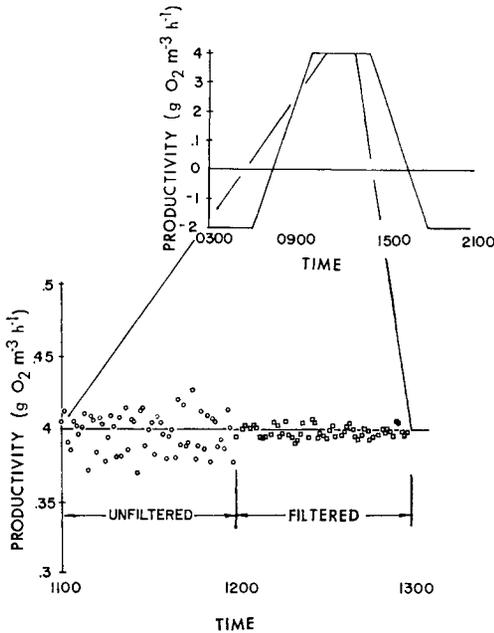


Fig. 1. Oxygen productivity calculated with Fourier transform method using simulated, noise-corrupted data with and without filtering. Inset shows entire productivity curve used in the simulation; only that portion of calculations from 1100 to 1300 is shown in main figure.

(chlorophyll *a* and pheophytin *a*) will be given elsewhere.

At two stations on the river, the signals from a galvanic cell oxygen probe (Precision Sci.) and thermistor were amplified, digitized, and recorded on tape every 15 s. Total solar radiation was similarly recorded from a pyrliometer at one of the stations. The data were reblocked, averaged (on a 1-min basis), and stored on cards as actual values of temperature and O_2 concentration. Amplified signals from the sensors range from 0 to 1,000 mV. Examination of the continuous output from the probes in situ reveals that, for a period of several hours, the signals may be recorded with a precision of ± 1 mV. This corresponds roughly to a precision of ± 0.01 $g O_2 m^{-3}$ in the recorded data.

Data processing—Because frequency, (ω), appears as a multiplicative factor in the numerator of Eq. 7, high frequency noise due to the random fluctuation of the least

significant recorded digit will be amplified. To avoid calculating rates of oxygen exchange on the basis of these fluctuations, it is necessary to filter the field data. We use "normal curve smoothing" with a 5-min filtering interval. Our technique uses a centrally weighted, moving average, where the weights are proportional to the ordinates of the normal probability density function. This form of smoothing has desirable properties (for the purpose of time-series analysis): the mean is unaltered and the phases of frequency components in the filtered series are not shifted relative to those in the original series (see Holloway 1958).

We investigated the effectiveness of this type of smoothing in decreasing the effects of random noise with a simulation. "Perfect" oxygen data were generated by substituting an assumed productivity function into Eq. 1. Data points were generated at 1-min intervals and randomly corrupted to simulate the precision indicated above. Figure 1 shows a comparison of the actual productivity used in the simulation and a portion of the productivities calculated from the noise-corrupted data with and without filtering. The values of productivity calculated from the filtered data are acceptably accurate, showing a maximum deviation between actual and calculated values of $0.01 g O_2 m^{-3} h^{-1}$; those calculated from the raw data show a maximum deviation of $0.03 g O_2 m^{-3} h^{-1}$.

Time series analysis—The relationships between oxygen and radiation and between productivity and radiation were examined using time-series analysis. The method estimates the frequency transfer function between two stationary stochastic processes within a limited range of frequencies. The range is determined by the width of the "lag window" and the data collection interval. The shapes of the gain, phase, and coherency spectra are diagnostic of the differential equation relating the two processes in which radiation and productivity (or oxygen) are viewed as the input and output respectively of a dynamic linear system. Jenkins (1965) reviewed the inter-

pretation of gain, phase, and coherency spectra for the purpose of systems identification. Platt and Denman (1975) reviewed the principles of spectral analysis and concept of lag windows and gave several examples of the method applied to ecological problems. Jenkins and Watts (1968) discussed both theoretical and practical aspects of the method.

The existence of trends in data records may cause problems in the analysis by over-emphasizing low frequencies and thereby obscuring the results (Platt and Denman 1975). For this reason all of the series used in the analysis were prefiltered by the first difference filter (Jenkins and Watts 1968; Holloway 1958). The BMD autocovariance and power spectrum program (Dixon 1968) was used to estimate the frequency transfer functions.

Results

Examination of the data showed that the diel curves of temperature and oxygen concentration recorded at the two river stations were similar, and we assumed that single station analysis could be used. The reaeration coefficients for the data used here are given in Hornberger et al. (1976) and were determined by the method of Hornberger and Kelly (1975).

Four days of data were chosen for analysis. These included two clear-sky days, 30 July 1973 and 4 August 1973, for which the light-productivity plots given by Hornberger et al. (1976) showed high correlation between light and productivity, and two noisy-radiation days, 12 and 13 August 1973, for which the correlation was reduced.

The smoothed, 1-min data were used to calculate productivity at 1-min intervals by the Fourier transform method. Fifteen-minute averages of the resulting productivities and of the radiation data were computed for 30 July 1973 and graphed (Fig. 2) to show the diurnal variation in productivity. For each of the other 3 days 2-h segments were chosen during which the radiation varied rapidly. The productivities calculated at 1-min intervals during these

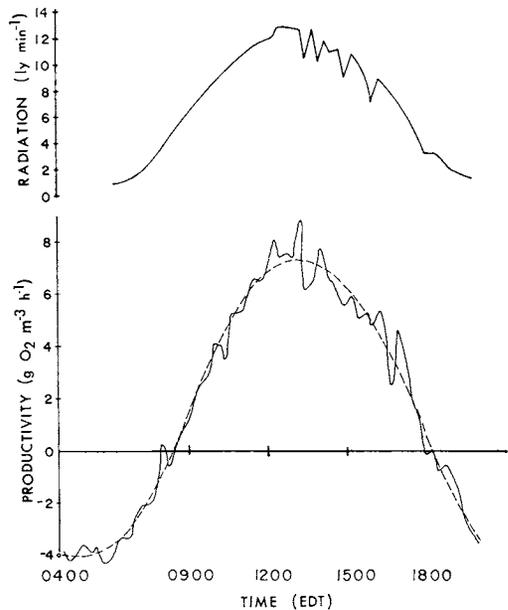


Fig. 2. Oxygen productivity and radiation vs. time, 30 July 1973. Solid curve shows 15-min averages of net productivity calculated by Fourier transform method with data at 1-min intervals. Dashed curve shows productivity calculated by Fourier series method with data at 30-min intervals.

segments are graphed in Fig. 3 along with smoothed, minute-by-minute averages of radiation.

Figure 2 shows that the productivity calculated using the Fourier transform method with data at 1-min intervals follows the diurnal trend calculated using a Fourier series (Kelly et al. 1974) with half-hour averages of the data. The calculations produced by the Fourier transform method are generally noisier than those of the Fourier series method, but the oscillations in the former appear more pronounced when the sky is not clear and radiation is not varying slowly.

Similar results were obtained for the mid-day portions of 4, 12, and 13 August 1973. Figure 3 shows that large fluctuations in community photosynthesis may occur over intervals of several minutes and that these are correlated with rapid changes in solar radiation, particularly on the last 2 days.

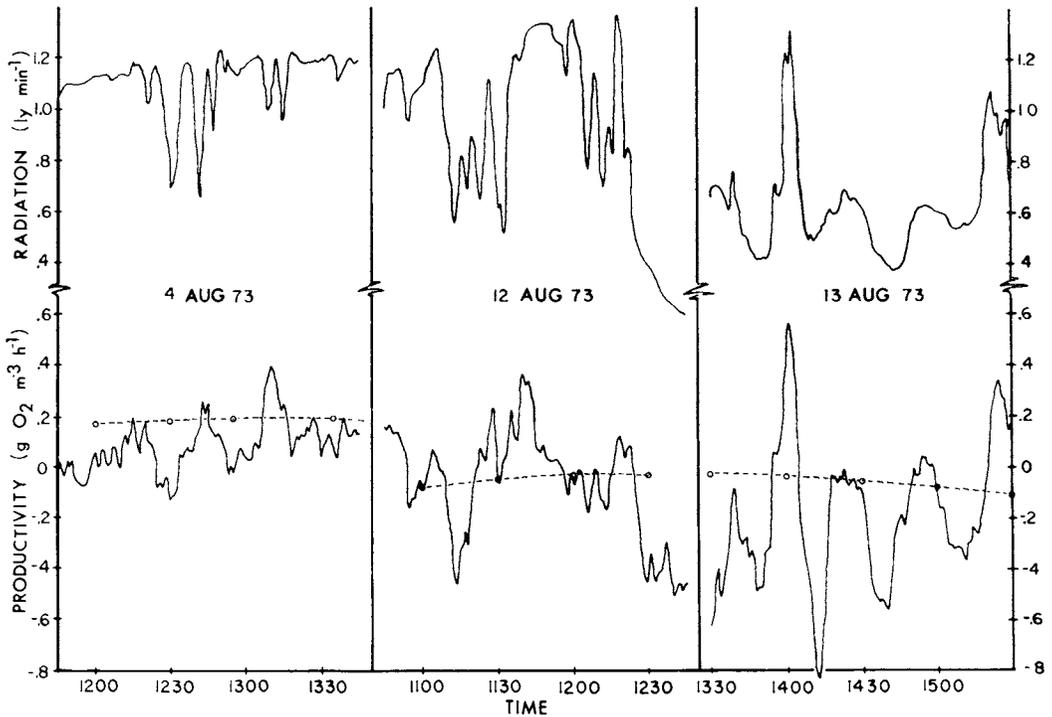


Fig. 3. Traces of incident radiation and oxygen productivity calculated with Fourier transform method at 1-min intervals for 2-h portions of 4, 12, and 13 August 1973. Dashed curves show Fourier series calculations of productivity for same periods.

We investigated the productivity–light relationship for 12 and 13 August 1973 further using spectral analysis. The gain, phase, and coherency spectra for radiation and productivity calculated for 12 and 13 August 1973 are shown plotted against frequency in Figs. 4 and 5. The gains are plotted on a log-log scale and phase on a semilog scale to conform with the usual presentation of Bode plots (Jenkins and Watts 1968). The lowest frequency estimate obtainable was $0.01 \text{ cycle min}^{-1}$ and the highest was $0.5 \text{ cycle min}^{-1}$, corresponding to fluctuations on time scales of 1.67 h and 2 min.

Coherency remains high out to a frequency of $0.2 \text{ cycle min}^{-1}$ and therefore the transfer function can be interpreted with confidence within a range of time scales from 1.67 h to 5 min. The filtering of field data necessary to obtain reasonably smooth estimates of oxygen exchange may

limit the detection of responses on time scales shorter than 5 min. The gain plots in Figs. 4 and 5 show that fluctuations in radiation input on time scales ranging from 30 min to 5 min are amplified in the net oxygen exchange output relative to variations on time scales longer than 1 h. The phase plots show that, within the same range of time scales, the output tends to lead the input by a phase difference of $+\pi/2$. These characteristics indicate that algal productivity responds to the time derivative of the radiation input (Jenkins and Watts 1968) within the range of frequencies that could be investigated by this method. Figure 2 shows that the diurnal component of net productivity (represented by the Fourier series method) is in phase with the diurnal component of the radiation curve. Thus on time scales of 12 h, the phase difference between output and input approaches zero.

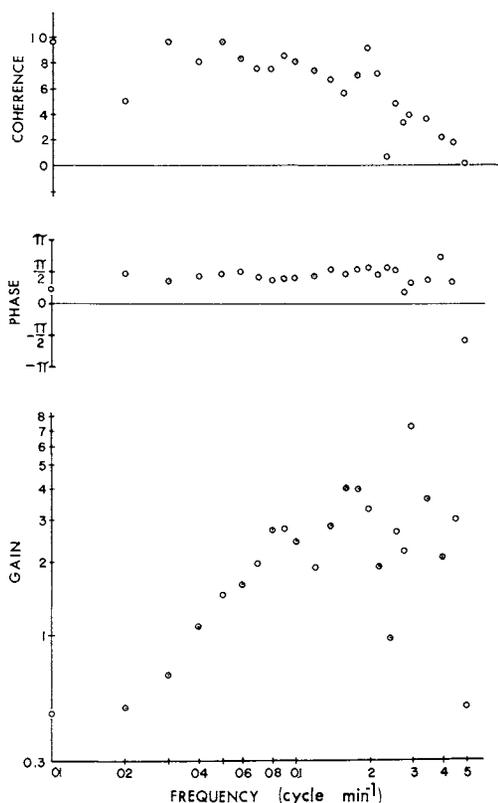


Fig. 4. Gain, phase, and coherency spectra between time series of incident radiation (input) and net productivity (output), 12 August 1973. A positive phase angle indicates that output leads input.

When we consider the full range of time scales from 12 h to 5 min, these results strongly suggest a linear lead system relating net productivity to light (Jenkins and Watts 1968). The continuous form of the differential equation for such a system would be (Jenkins 1965)

$$[P-R](t) = g \left[I(t) + T \frac{dI(t)}{dt} \right] \quad (8)$$

where $[P-R](t)$ = net community productivity as a continuous function of time ($g \text{ O}_2 \text{ m}^{-3} \text{ h}^{-1}$); $I(t)$ = solar radiation as a continuous function of time (ly min^{-1}); g = steady state gain of system [$(g \text{ O}_2 \text{ m}^{-3} \text{ h}^{-1})(\text{ly min}^{-1})^{-1}$]; T = time constant (h). The steady state gain of the system is

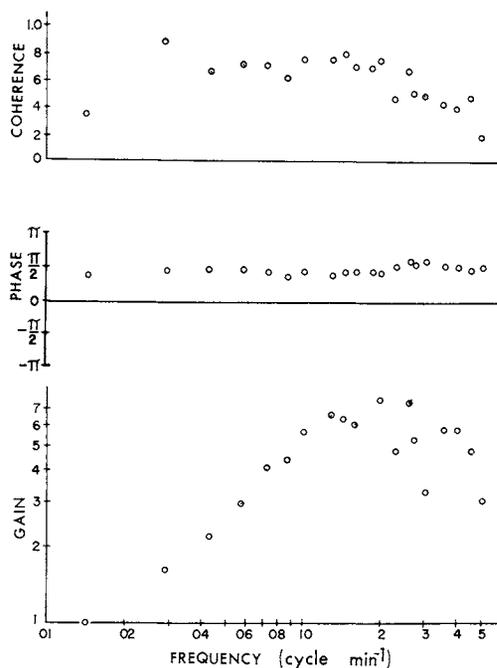


Fig. 5. As Fig. 4, 13 August 1973.

essentially the slope of the diurnal light-productivity plot in the absence of rapid fluctuations in solar radiation. The time constant, T , controls the rate of decay of $[P-R](t)$ to its steady state rate following a step change in light. This model clearly explains the deviation of productivity from the direct proportionality model during episodes of changing light. During clear sky conditions dI/dt is very small and a linear productivity-light curve results. This relationship is detected by the Fourier series method (Kelly et al. 1974) and represents the steady state response of the system. However, with patchy clouds dI/dt is highly variable in both magnitude and direction, and net productivity fluctuates above and below its steady state rate with greater amplitude than would be predicted by a directly proportional response to radiation levels. The result of these fluctuations is that the highest rates of oxygen production do not necessarily correspond to the highest radiation levels (see Fig. 3, especially 12 August) and the lowest rates of

oxygen production do not necessarily correspond to the lowest radiation levels (*see Fig. 3, especially 13 August*).

Discussion

The Fourier transform method presented above provides a new way to determine productivity from dissolved oxygen measurements. It can efficiently handle large amounts of data and can therefore be used with nearly continuous records of field data to study short term variations. In principle, previously used methods of analyzing free-water dissolved oxygen records may be used to accomplish the calculations presented here, but the noise-enhancing properties of the finite-difference method of Odum (1956) and the large amount of computer time and storage required to detect short term variations by the Fourier series method (Kelly *et al.* 1974) make such analysis by these methods impractical.

The question of whether these results could be due to some artifact cannot easily be completely resolved, but we feel that there are strong indications that actual variation in oxygen exchange is being measured. The results using noise-corrupted simulated data indicates that normal instrumentation noise should not obscure changes in net oxygen evolution and that dissolved oxygen can be recorded with sufficient precision to infer minute-to-minute changes in rates of oxygen exchange. This is borne out by results obtained during slowly varying light conditions on clear-sky days. Application with field data shows that the predicted fluctuations in photosynthesis correspond to periods of rapidly varying radiation, and this also supports the contention that recorded data actually reflect differences in rates of oxygen evolution. It is of course possible that oxygen concentration is being influenced by some light-dependent factors other than photosynthesis. The only possibilities we can conceive are nonbiological photochemical reactions and changes in reaeration rate. There are no known photochemical reactions that occur in natural waters and influence oxygen concentration, and there is no known physi-

cal mechanism that would cause the reaeration rate to be correlated with sunlight.

The linear lead model relating net productivity to radiation suggests that net oxygen evolution is sensitive to both the level of radiation and the rate of change of radiation. Such a response is common among biological receptors and is strong evidence that oxygen evolution by an algal community is regulated by a dynamic control system (Milsom 1966). The response to the time derivative of the input signal is called "rate sensitivity." These systems respond more rapidly to changes in input than systems with simple proportional response (Milsom 1966). This is significant for an algal community in a fluctuating light environment since rate sensitivity allows the community to attain its steady state photosynthetic rate faster than would be possible by a proportional response alone. Rate sensitivity cannot cause the mean rate of oxygen evolution to be higher than that in a system without such control; the rate-sensitive term in Eq. 8 responds to both increases and decreases in radiation. However, a rate-sensitive response to light allows the community to track changes in radiation input without the phase lag incurred by a pure gain response with its associated time delay (Milsom 1966). This type of response would certainly be adaptive for the species of a plant community since, for example, it would allow a quick response to brief sunny periods on otherwise cloudy days.

Free-water measurements of oxygen exchange on brief time scales are available only for a river community, but the predominance of diatoms in the Mechums River suggests that the linear lead phenomenon may be important for phytoplankton in near-surface oceanic waters which circulate through a vertical light gradient on time scales as rapid as those reported here. If the rate-sensitive response does indeed occur in phytoplankton communities, changes in photosynthetic oxygen production would occur due to circulation, even within the light-saturated zone, that would not be measured by light-dark bottle tech-

niques. As for a river community, the response would also be advantageous for phytoplankton because of the varying light environment.

The methods available for studying the variations in community productivity in natural waters do not enable us to speculate about the physiological mechanisms responsible for the control system hypothesized. The model obviously lumps together many complex biochemical processes, and the parameters cannot be associated with any single mechanism. The advantage of this treatment is that it provides a simplified view of the performance of the total system and identifies speed of response as an important characteristic for the algal community.

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