OBSERVING AND UNDERSTANDING THE DYNAMICS OF ALGAL PHOTOSYNTHESIS AND RESPIRATION

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REFERENCE: Proceedings of the 2001 Georgia Water Resources Conference, held March 26-27, 2001, at the University of Georgia. Kathryn J. Hatcher, editor, Institute of Ecology, the University of Georgia, Athens, Georgia.

Abstract. Experimental manipulations of an aquaculture pond have been observed using the University of Georgia's Environmental Process Control Laboratory. The data, which are comprehensive, cover a continuous five-month period with a very high sampling frequency (of the order of minutes); variables observed include solar radiation, several nitrogen species, orthophosphate-P, chlorophyll-*a*, dissolved oxygen, and pH. A small portion of these data – for a period of some 15 days in August, 2000 – are examined in detail. The goal is to extract the periodic (diurnal) components of the observed time-series signals, using recursive estimation algorithms, with a view to identifying significant matches and differences among the phases of these extracted components. Ultimately, the objective is to observe and understand the fast dynamics of algal photosynthesis and respiration *in situ*; our contention is that clearly identifying phase differences among the diurnal signal fluctuations contributes substantially to reaching this goal.

INTRODUCTION

Modeling the dynamic behavior of environmental systems can be approached from the perspective of theory or from that of the observed data. Considerations of both are indispensable to developing a working and useful understanding of such complex systems. In practice, all models are neither perfect articulations of current theory nor perfect representations of what has been observed in the field. Here, following an earlier study (Stigter *et al*, 1997), we take a further step towards developing and confirming a theory-based understanding of algal photosynthesis and respiration through a data-based, signal processing procedure. In presenting these preliminary results – for the analysis of a comprehensive set of field data – we note that several theory-based, or "mechanistic" models of algal photosynthesis and respiration are already available. Our analysis is self-evidently entirely geared to a particular set of data and to interpretations, *at this stage*, that will make little reference to that body of theory. Reconciling that theory with our field data, however, is our ultimate objective.

METHOD

Equation 1 is the simplest expression of the Dynamic Harmonic Regression (DHR) model, which only consists of trend (T_t), seasonal (S_t) and white noise (e_t) components.

$$y_t = T_t + S_t + e_t \quad t = 1, 2, \ldots, N \qquad (1)$$

in which,

$$S_t = \sum_{i=1}^{R} S_{i,t} = \sum_{i=1}^{R} \{a_{i,t}\cos(\omega_i t) + b_{i,t}\sin(\omega_i t)\}$$

where, $a_{i,t}$, $b_{i,t}$ are stochastic *time varying* parameters and ω_i, $i = 1, 2, \ldots R$, are the fundamental and harmonic frequencies associated with the seasonality in the series. The DHR model can be considered as a straightforward extension of the classical, constant parameter, Harmonic Regression (or Fourier series) model, in which the gain of the harmonic components ($S_{i,t}$) can vary as a result of estimated *temporal* changes in the parameters $a_{i,t}$ and $b_{i,t}$ (Young, 1998).

A massive data base has been retrieved from a small (0.71 ha) aquaculture pond at the Whitehall estate of the University of Georgia's School of Forest Resources. The School's Environmental Process Control Laboratory, together with supporting monitoring facilities (Hydrolab mult-parameter datasondes, Turner fluorometers), have been deployed from May 22nd through October 16th, 2000, in order to acquire comprehensive and detailed time-series observations with a sampling frequency of the order of 15 minutes or less. The data sets used in this paper are chosen from the window of August 13th to August 27th,

2000. For computational reasons, all the data were decimated every eight samples. Twelve water quality variables were measured, including orthophosphate-P (PO_4-P), ammonia-N (NH_3-N), total oxidizable carbon (TOC) and total oxidized nitrogen (TON) (as nutrients), photosynthetically active radiation (PAR), temperature, pH, dissolved oxygen (DO), conductivity, oxidation-reduction potential (ORP), and suspended solids (SS) (as physico-chemical variables), and one biological variable, i.e. chlorophyll-*a* (Chla).

Not surprisingly, the spectral analysis strongly demonstrates that all these time series (except that of suspended solids) contain dominant diurnal and semi-diurnal harmonic components. We model the trend (T_t) as a Smoothed Random Walk (SRW) and the four *time varying* parameters ($a_{i,t}$ and $b_{i,t}$, i=1, 2) associated with these two harmonics as Random Walks (RW) to allow for possible changes *with time* in the amplitude and phase of these terms over the 15-day period (Young, 1990). Figure 1 shows the raw data, interpolated data of DO, and the extracted trend, and Figure 2 shows the extracted diurnal and semi-diurnal periodic signals. It is especially important to note that with this particular type of analysis, using recursive estimation algorithms, it is possible to extract periodic oscillations with a *time-varying* amplitude (as apparent from Figure 2). Further, we note in passing that Figure 1 shows how the feature of signal smoothing incorporated into the underlying algorithms allows interpolation across gaps in the original, raw, time series. The data (apparently) missing from the record on 18 August in Figure 1 have in fact been deliberately removed in order to illustrate this capability. The same DHR analysis has been applied to the other 11 time series.

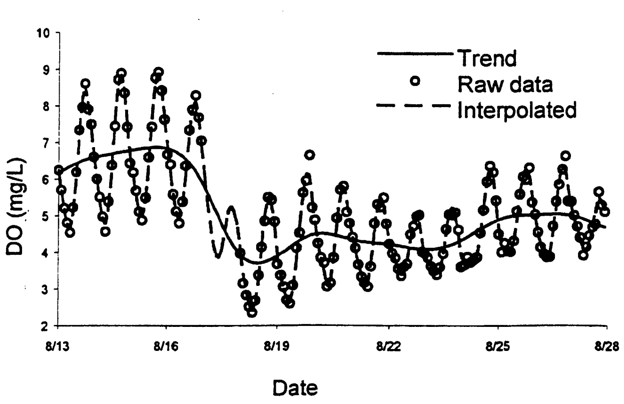

Figure 1. Raw data, interpolated data and trend of DO time series

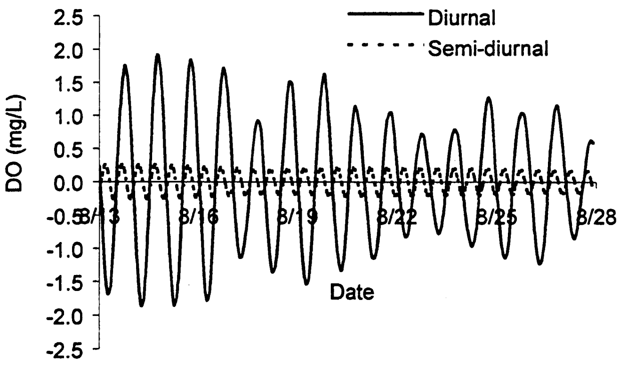

Figure 2. Extracted diurnal and semi-diurnal harmonic components of DO time series (negative values are present because the components are deviations about the extracted trend)

RESULTS AND DISCUSSION

Figure 2 shows that the diurnal oscillation is a dominant contribution to the harmonic components. For simplicity, we only utilize the diurnal oscillation component as a vehicle to explore the relationships among the observed physical, chemical and biological variables in the aquaculture pond.

Table 1. Peak and trough times of all variables (24 hour clock)

Variables	Peak	Trough
Solar radiation	14	2
Temperature	20	8
Suspended solid	-	-
PH	18~20	6~8
Conductivity	8~10	20~22
Redox	6~8	18~20
Dissolved oxygen	18	6
Ammonia-N	6~8	18~20
Total oxidized nitrogen	16	4
Total inorganic nitrogen	14	2
Orthophosphorate-P	12	0
Total oxidizable carbon	12	0
Chlorophyll-*a*	22~2	10~14

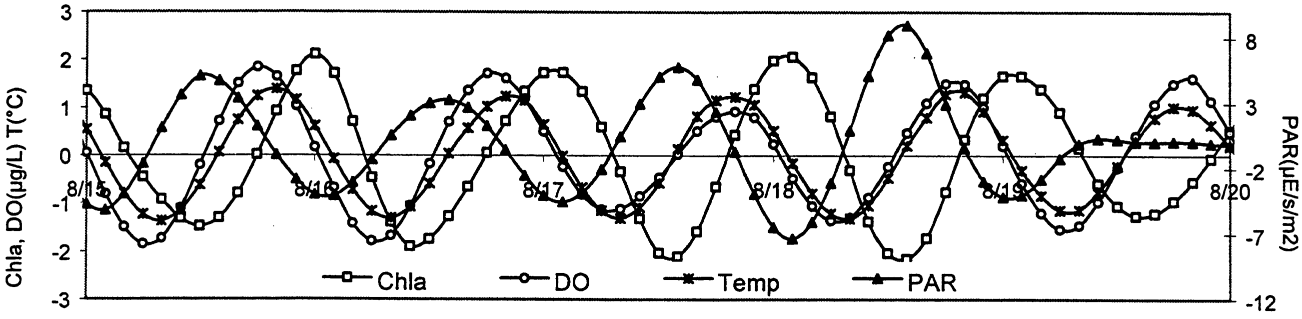

Figure 3. Solar radiation as a driving force of a small pond system

Inspection of the diurnal variations extracted through the DHR analysis allows the timings of the peaks and troughs of all measurable variables to be identified, as given in Table 1. Over these 15 days in late August, the diurnal cycles of some variables shift back and forth some 2 to 4 hours, especially chlorophyll-*a*, which is an indicator of the amount of algae in the aquaculture pond.

Solar radiation as a driving force

Solar radiation (photosynthetically active radiation, PAR) is one of the most important water quality variables, and also strongly affects other water quality variables (Boyd, 1990). Figure 3 shows that solar radiation as a driving force of a small aquaculture pond system affects temperature (physical variable), dissolved oxygen (chemical variable), and chlorophyll-*a* (biological variable) with different response times. For the purpose of illustration, Figure 3 displays only 6 days (as in Figures 4 and 5 below).

In most aquaculture pond systems, solar radiation is the only factor directly influencing water temperature. Dissolved oxygen concentration is affected indirectly by solar radiation through the processes of photosynthesis and respiration. In the late morning and towards noon, before solar radiation reaches a peak, we suggest that photosynthesis begins to be more and more active than respiration, so that more and more oxygen is released into the water body, and chlorophyll-*a* (indicating the biomass of algae) also starts to increase. About 6 hours later, as more and more algal biomass is produced, respiration begins to exceed photosynthesis, hence dissolved oxygen reaches a maximum and starts to decline. Figure 3 also shows that even though the dissolved oxygen begins to decline at around 18:00 (4 hours after the PAR peak) in the evening, the value of chlorophyll-*a* still increases until the solar radiation comes down to approximate zero near midnight (about 10 hours after the PAR peak), which suggests that the release of oxygen and the growth of algal biomass are not simultaneous.

Chlorophyll-*a* and nutrients

Figure 4 (a) shows the phase relationships between algae (as indicated by chlorophyll-*a*) and the concentrations of nutrients. When the biomass of algae in the pond is at a maximum, the nutrients in the water body, including orthophosphate-P, total inorganic nitrogen (TIN, summation of NH_3-N and TON) and TOC, are likely to have been incorporated into this cell matter to a maximum extent; hence the concentrations of these nutrients tend to be at a minimum. Interestingly, the extracted diurnal components for chlorophyll-*a* and orthophosphate-P have directly opposite phases, whereas those of TIN and TOC are respectively slightly less than and slightly more than180 ° out of phase.

Given the independent measurements of total oxidized nitrogen (TON) and ammonium-N it is possible to examine the phase difference between chlorophyll-*a* and TIN in a more detailed manner, as shown in Figure 4 (b). Given the complexity of the nitrogen cycle – in particular, the possibility of confounding activity from any accompanying bacterially mediated nitrification and denitrification – it is not easy to draw conclusions from Figure 4 (b). However, if anything, our results suggest ammonium-N is taken up by the algal cell matter somewhat before TON (within the diurnal cycle, that is).

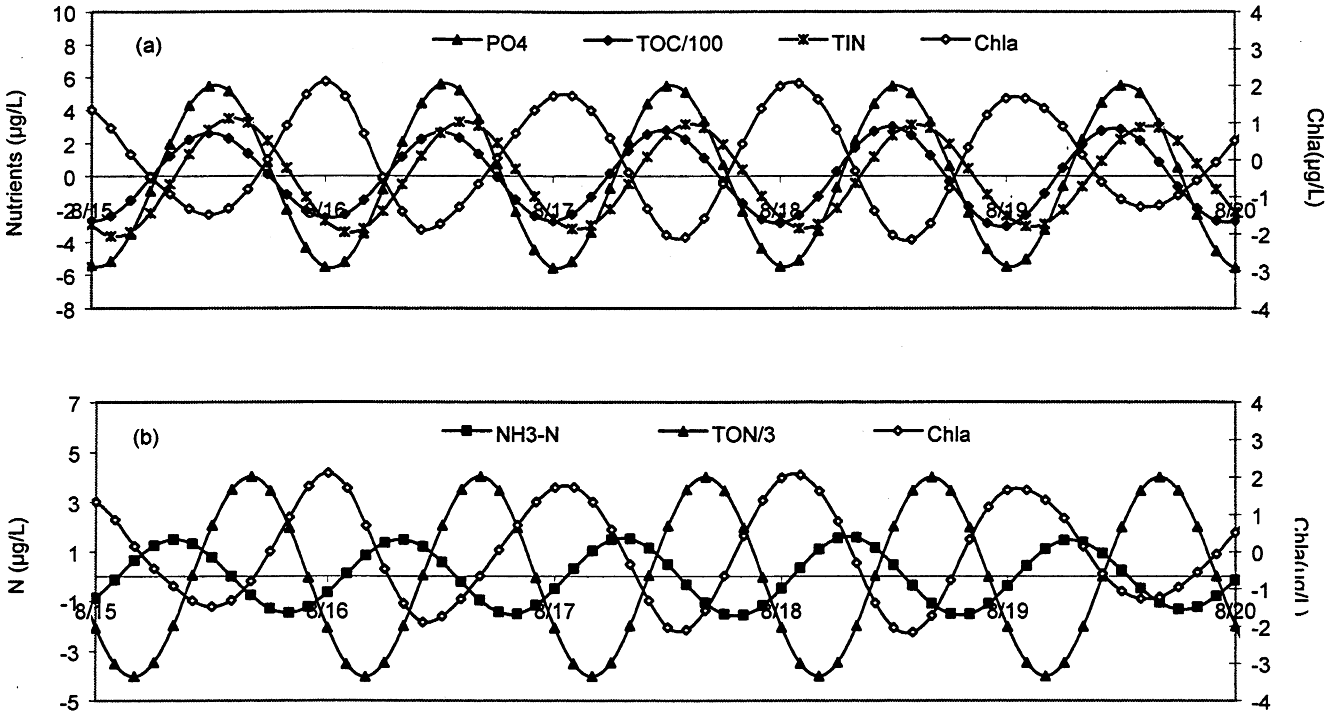

Figure 4. Phase lags between diurnal signals of chlorophyll-*a* and nutrients

CONCLUSIONS

In an intensively observed pond experiment all variables, with the exception of suspended solids, exhibit discernible diurnal fluctuations. If one attempts to compare and contrast the details of these fluctuations using the original (raw) data, *without* their respective longer-term trends having been removed (as well as *without* smoothing), it is difficult to acquire the kind of preliminary insights discussed above. Of special importance in our analysis has been the capacity to track variations *with time* in the amplitudes of these (diurnal) oscillations, which again permits, in principle, more incisive interpretation of the possible mechanisms underpinning observed behavior. Our results are indeed preliminary. As yet they are not sufficient to provide more detailed guidance on how we might begin to assemble some basic mechanisms of algal photosynthesis and respiration for incorporation into a theory-based model. We believe they are encouraging, nevertheless, and offer the promise of our being able to proceed further in that direction.

LITERATURE CITED

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