Model methods for the analysis of mesocosm experimental studies

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ABSTRACT: The response of experimental ecosystem dynamics to varying nutrient loads was studied by analysing oxygen time-series. Time-series had been continuously recorded, and the data were analysed on a daily basis using a computer model which describes basic oxygen processes. The resulting sets of production and consumption parameters described the dynamic characteristics of each basin during the experimental period of 180 days. Dynamical analysis appeared to be possible; although the results did not indicate a clear relationship between oxygen dynamics and nutrient supply in these systems.

INTRODUCTION

There are many tools and methods available to study ecosystems and ecosystem processes. They vary from large-scale ecosystem studies in the field to studies on a single species in the laboratory. Mesocosms are considered to be the link between these two extremes. Such medium-scaled experimental enclosures integrate many processes, but may still be controlled to a certain extent. The results resemble reality more than laboratory experiments do, due to the more natural behaviour of organisms (Brock et al., 1993).

Mesocosms, or model ecosystems, often are applied to study the system's reaction to a variety of input conditions such as nutrient load, temperature, insolation, or even pesticides. The natural system behaviour in mesocosms, or the system's reaction to varying input conditions is generally studied by monitoring chemical and biological state variables, such as phosphorus concentration, algal cell numbers and benthic filter feeder biomass or numbers (Bratbak et al., 1993; Carlsson & Granéli, 1993; Doering et al., 1989; Hansen & Blackburn, 1991; Hinga, 1992; Vanni & Findlay, 1990; Widbom & Elmgren, 1988). These results may be analysed using (multiple) regression analysis techniques and non-deterministic models such as time-related polynomes (Roberts, 1992). However, these methods generally stress the state of the system, rather than the dynamic interrelations. Other methods quantify processes in such systems, such as primary production rates, sediment/water fluxes of inorganic compounds and zooplankton community filtering rates (Niederlehner & Cairns, 1990; Keller et al., 1990; Kelly et al., 1985; Nilsson et al.,

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1991; Oviatt et al., 1986; Sampou & Oviatt, 1991; Sullivan et al., 1991). Such processes are generally directly measured. The application of dynamic model analysis may also be considered: dynamic characteristics of the system are found by fitting dynamic model results to experimental data such as state variables and/or process rates. Most promising so far is the analysis of oxygen time series that leads to a quantification of oxygen production and consumption in the system (Van Straten, 1986; Van Straten & Kouwenhoven, 1991; Keesman, 1989; Kouwenhoven, 1994). Oxygen is used because concentrations can automatically be assessed, resulting in hundreds of data per system per day.

MATERIAL AND METHODS

Outdoor marine mesocosms were constructed on the island of Texel in order to study shallow estuarine ecosystems, such as the Wadden Sea. These eight experimental basins were used in 1992 to examine the system's responses to changes in environmental conditions regarding nutrient loads (Benthic Eutrophication STudies: BEST), with special emphasis on the hypertrophic situation in the Venice Lagoon in Italy. The mesocosms were installed to closely resemble a relatively unpolluted situation in the Venice Lagoon. During this experiment, several biotic and abiotic state variables and processes were regularly measured, at least once every 5 weeks, in all mesocosms. In addition, oxygen concentrations, insolation and temperature were frequently measured, viz. every 30 seconds.

This paper concentrates on the oxygen data analysis. The objective is to derive daily parameters from these time-series in order to characterize the dynamic behaviour of each system during the research period. This implies that the available biotic data remained unused in this stage of the analysis.

Basic processes included in the oxygen model were production and consumption of oxygen and oxygen exchange between atmosphere and water. In complex ecosystem models, the description of both of the first processes may become very complicated, considering different kinds of primary producers and consumers. Here, it was assumed that the chemical and biotic system characteristics did not change during each daily analysis. This is a very crucial assumption, implying that each single analysis should be restricted to such a relatively short period. The length of this period cannot be shorter than one day, because the complete 24-hour oxygen concentration cycle is to be analysed to cover both production and consumption. If the period were somewhat longer, the assumption of constant biotic concentration would become less realistic. The experiment lasted 180 days. Thus, for each of the eight systems, 180 daily parameter sets became available that supplied information on the system dynamics in terms of oxygen production and consumption. These parameters vary during the season and are expected to be different for each basin. They contain information on the underlying biotic variables, and should, therefore, reflect the different reaction of each basin to the experimental treatment.

Mesocosm setup

Eight 21-m^2 basins with 0.55 m water depth and 0.5 m sediment were set up identically, the only difference being the additional nitrogen and phosphorus input of each system (Fig. 1[1]). The basins were continuously flushed with Wadden Sea water. The
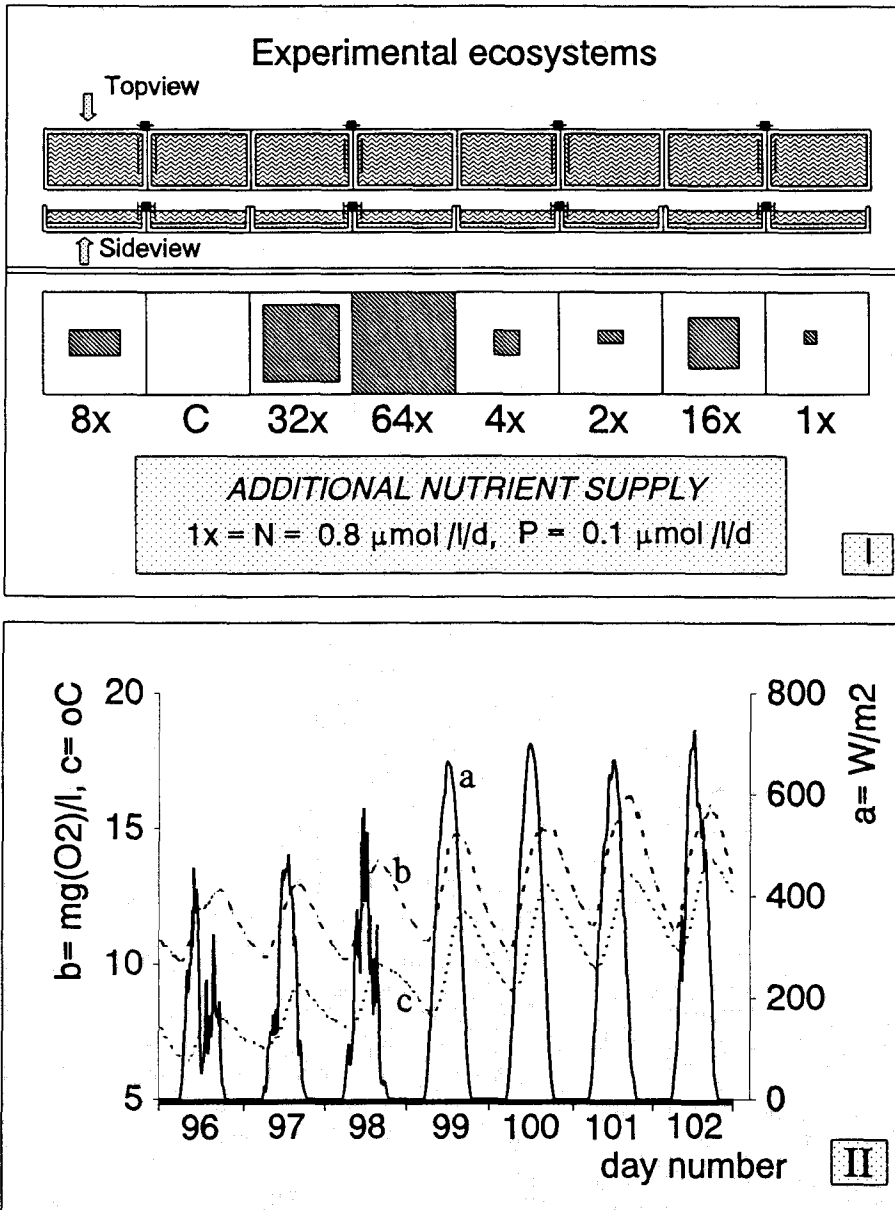
Fig. 1. I: Experimental setup: experimental basins, with position of wave boards and addition of nutrients to each basin; II: data for days 96–102 in 1992; a = solar insolation $(W \cdot m^{-2})$; b = oxygen concentration $(mg\ O_2 \cdot l^{-1})$; c = water temperature (°C)

residence time of the water in a basin was 6.5 days. The response of the mesocosm ecosystems to the different nutrient additions was monitored from March to September 1992. Oxygen concentration (WTW OXI219 + Trioxmatix 600/130 oxygen probe), insola-

tion (Licor LC-Li 200SB pyranometer) and water temperature were measured every 30 seconds, and 15-minute averages were recorded (Fig. 1[II]) on a 14-bit Campbell CR10-64k datalogger. Wind data at 10 m standard height was provided by the Royal Dutch Meteorological Institute (KNMI, 1992), recorded at the nearby weather station at "The Kooy" Airport (Den Helder). The basins are referred to as Mxx, where xx is the nutrient addition (M00, M01, ..., M64).

MODEL ANALYSIS

Basic oxygen model

In the mesocosm study, the production of oxygen results from the assimilatory activities of macroalgae and pelagic and benthic microalgae. The intensity of the oxygen production is a function of a number of environmental conditions:

$$\text{Production} = f(\text{light, temperature, nutrients, algae, ...}) \tag{1}$$

The assumption that the nutrient concentrations and algae densities had not changed during each day, implied that light and temperature had been the only important factors. For the model, it was also assumed that F(temperature) = 1:

$$\text{Production} = \mu_{max} \cdot F(\text{light}) \tag{2}$$

the factor μ_{max} combined all the other variables excluding light. The production-light relationship was kept as simple as possible and started with a somewhat rough approximation:

$$\text{Production} = q \cdot I_0 \quad (\text{mg } O_2 \cdot l^{-1} \cdot d^{-1}) \tag{3}$$

where I_0 was the global radiation (W·m^{-2}). Thus, q (mg $O_2 \cdot l^{-1} \cdot \text{day}^{-1} \cdot (W \cdot m^{-2})^{-1}$) contained all the other relationships.

Consumers include benthic and pelagic bacteria that degrade organic matter (detritus), and respiring algae and benthic and pelagic animals.

$$\text{Consumption} = f(\text{temperature, mineralization, ...}) \tag{4}$$

Consumption includes all the respiratory activities and all the bacterial mineralization processes. The first depends on the activity and contents of algae and fauna species; the second is determined by the content and composition of the detritus. Oxygen consumption takes place in the water and in the sediment. Although temperature is a key variable here, it was assumed that F(temperature) = 1:

$$\text{Consumption} = R \quad (\text{mg } O_2 \cdot l^{-1} \cdot d^{-1}) \tag{5}$$

R being the sum of all consumption processes.

Exchange of oxygen across the atmosphere/water interface is the physical key process that controls the oxygen content in the water:

$$\text{Reaeration} = k_r \cdot (C_\infty (\text{sal, T}) - C(t)) \quad (\text{mg } O_2 \cdot l^{-1} \cdot \text{day}^{-1}) \tag{6}$$

where k_r was the reaeration coefficient (day^{-1}) and C_∞ (sal, T) the oxygen saturation concentration in the water. The temperature (T) and salinity (sal) dependencies of C_∞

were taken into account (see e.g. APHA, 1985). k_r itself is also temperature-dependent, but the variation with temperature is much smaller than that of C_∞.

Thus, the model reads

$$\frac{dC(t)}{dt} = q \cdot I_0\ (t) - R + k_r \cdot (C_\infty\ (sal,\ T) - C\ (t)) \qquad (mg\ O_2 \cdot l^{-1} \cdot day^{-1}) \qquad (7)$$

Input/output processes were not included in this analysis, since the time constant for these processes was about 1 week, which was much larger than that of the processes mentioned here: $O(\tau) = 1$ day.

Data analysis

The parameters q, R and k_r had to be estimated from the oxygen time-series (Figure 1^{II}). Two methods were applied:

(1) differential equation (7) was numerically solved, and the computed oxygen concentrations were compared with the data (C_m). Usually, C(t = 0) was also estimated, since it cannot be assumed that C(t = 0) is exactly known. For this method, the STEM software package was applied (ReMeDy, 1991), using a Nelder-Mead (simplex) minimization procedure which is robust although not very time efficient (Kouwenhoven, 1994).

(2) differential equation (7) was solved from data-point to data-point following

$$\frac{\Delta C}{\Delta t} = q \cdot I_0\ (t) - R + k_r \cdot (C_\infty\ (sal,\ T) - C\ (t)) \qquad (8)$$

The analysis was started for each separate time interval $[t, t + \Delta t]$ with the measured situation at time = t. The difference between measured (C_m) and computed oxygen concentrations was much smaller in this second approach, since the computed prediction was limited to one time-step, which is 15 minutes in the time series.

The conditions for both operations are that C(t) and I_0 (t) are continuous and can be differentiated at $[t, t + \Delta t]$. Purely mathematically, this was not the case, because global radiation and C(t) were measured at discrete time intervals. However, biologically the influence is not discrete but is always some average of the present and the preceding conditions. Hence, it was assumed that equation (7) was mathematically valid for the biological system. From equation (8), it follows that

$$C(t+1) = (1-\Delta t) \cdot C(t) + \Delta t \cdot I_0\ (t) + \Delta t \cdot k_r \cdot C_\infty\ (sal,\ T) - \Delta t \cdot R \qquad (9)$$

had to be computed. The MATLAB scientific software (MATLAB, 1991) was used to solve equation (9).

In both cases, minimizing S, with

$$S = \sum_{t=1}^{m} R_t^2 = \sum_{t=1}^{m} (\hat{C}(t) - C\ (m,t)\ )^2 \qquad (10)$$

regarding the wanted parameters (q, R and k_r) yields best parameter values. C(m,t) is the measured value at time t. $\hat{C}(t)$ is the computed oxygen concentration at each time t.

Uncertainties

When applying a model, one has to be sure that the model is adequate, and that the data are sufficient to discriminate between the mentioned processes.

Data

The available oxygen time series C(m,t) were not exact. Two error sources are relevant: the instrumental error and the experimental error.

Model

The model is not complete; some errors remain. The true model reads

$$\frac{dC(t)}{dt} = q \cdot I_0 (t) - R + k_r \cdot (C_\infty(t) - C(t)) + v(t) \tag{12}$$

where v(t) is stochastic. v(t) is thought to be normally distributed, having an expected mean value of v(t) = 0. The study of the residues supplies information on v(t); the model may be assumed to be correct when v(t) has a white noise characteristic. If not, the residues may contain additional information. Equation (10) minimizes v(t).

Parameters

A model may be correct, but the collected data may not be sufficient to discriminate between all the described processes. Therefore, correlations between parameters have to be studied. This was done by computing.

$$S(\Theta) = S(\hat{\Theta}) \cdot [1 + \frac{p}{n-p} \cdot F (p, n-p, 1-\alpha)] \tag{13}$$

where $\hat{\Theta}$ was the parameter set minimizing S (equation 10), and Θ was the parameter set for which S obeys equation (13), for p parameters, n datapoints and a $100 \cdot (1-\alpha)\%$ confidence contour; F being the relevant Fisher's distribution value. The application of equation (13) caused a problem: the 96 observed oxygen concentrations per day were not independent. Thus, the value of n in equation (13) was much less than 96 when analysing the results of one day. There is not much literature available on estimating the uncertainty of time-series parameters. As a rough and optimistic estimate, it was assumed that a maximum of six parameters could be derived from the oxygen data. Thus, n = 6 and p = 3 in this analysis. The resulting contours were exact; the confidence value assigned to such a contour is approximate when the model is not strictly linear in all its parameters (Draper & Smith, 1981; Jansen et al., 1990). In this case, the estimated value for n (number of independent data-points) introduced a large extra uncertainty regarding the 'real' confidence value. Such contours show how well one can discriminate between the separate parameters by using the data that are collected. If necessary, the model may be adapted (without or by hardly changing the numbers of parameters), resulting in better discrimination properties.

Some model adaptations

Data uncertainties

Instrumental errors were tested by recording the output every 30 seconds. Short-term variations were found to exist at the level of the instrument's accuracy, about 2^{-14} times the maximum recorded value, so at the $\mu g\, O_2\, l^{-1}$ level. They were neglected in this research.

Experimental errors were tested by investigating the mixing characteristics in one of the basins. It was found that the mixing was sufficient to prevent local differences. It was concluded that the measurements represent the actual situation in all basins.

Model uncertainties

The model residues (v(t) in equation 12) contained some daily periodicity. Production seemed to be relatively larger during the morning than during the afternoon, or: oxygen consumption seems to be relatively larger during the afternoon. It is rather hard to discriminate between these two possibilities. A better result was obtained by the incorporation of a light limitation function:

$$F(I) = \left(\begin{array}{l} \dfrac{I}{I_k} \ : \ I < I_k \\ 1.0 \ : \ I \geq I_k \end{array} \right) \qquad (-) \tag{14}$$

where I_k (W·m^{-2}) is the photosynthetic parameter. A value of $I_k = 400$ (W·m^{-2}) was found to be appropriate. The production term (equation 3) now reads

$$\text{Production} = q^0 \cdot F\ (I) \qquad (\text{mg O}_2 \cdot l^{-1} \cdot d^{-1}) \tag{15}$$

where q^0 is the maximum productivity (when F(I) = 1.0). To compare q from equation (3) to q^0, one should read

$$q = q^0 \cdot \frac{\overline{F\ (I)}}{\overline{I}} \qquad (\text{mg O}_2 \cdot l^{-1} \cdot d^{-1} \cdot (\text{W·m}^{-2})^{-1}) \tag{16}$$

where F(I) and I are averaged over the 24-hour period.

Parameter uncertainties

Results for basin M08 are shown in Figure 2[I] for day 100. The STEM package was used, the model is represented by equation (7). It was first checked how the parameters were correlated. The combined approximately 90 % confidence contours for the three possible combinations are shown in Figure 2[II]. Although the individual confidence interval may be rather small, combinations of parameters allow a much larger deviation from the best estimates.

It turned out that during times of production (the oxygen concentration was generally above the saturation value, similar to the situation shown in Figure 2[I]), the k_r and the R parameter could hardly be separated, while during times of consumption (usually later in the year, when oxygen concentrations were generally below the saturation value) k_r and q were hard to separate.

Since the k_r-parameter depends mainly on wind speed, it was decided to use an empirical wind-k_r relationship to compute all k_r-values, instead of estimating them. In Figure 3, all estimated k_r-values are related to the measured wind speed UWI (m·s^{-1}) at 10 m standard height (KNMI, 1992):

$$k_r = \text{depth}^{-1} \cdot [0.517 + 0.129 \cdot \text{UWI}] \qquad (d^{-1}) \tag{17}$$

The constant term (0.517) in equation (17) was caused by the mechanical wave board
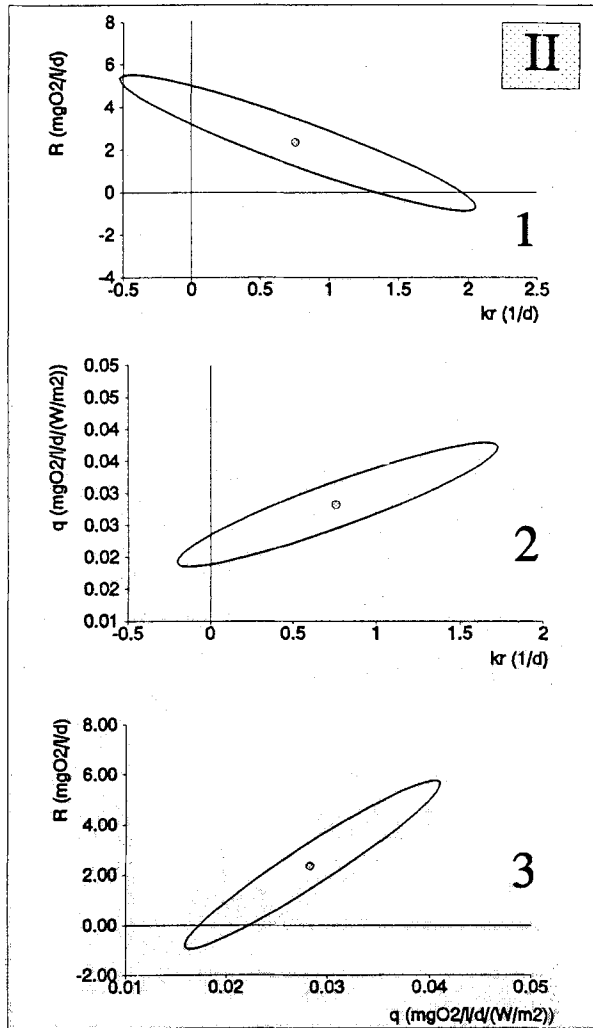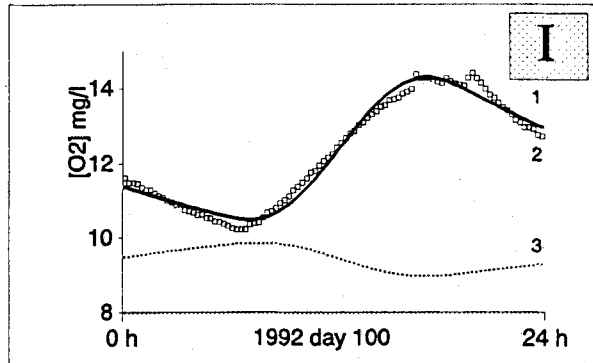
mixing in the basin. The k_r-values as shown in Figure 3 were not very different from the values resulting from Banks' review (Banks, 1975); only the sharp increase at higher UWI-values was not observed here. The scatter of k_r-values illustrates the variability in computation results. It was decided to compute k_r according to this empirical relationship: the rest of the analysis was done using equation (17). The result was that unrealistic values for k_r were avoided; at the same time, the resulting q- and R-values obtained more biological meaning.

RESULTS

In Figure 4, q^0 (maximum productivity) and R values are shown for basin M08 in 1992. It is obvious that neither the maximum productivity, nor the system's oxygen consumption show a smooth pattern during the experimental period. The occasionally rather abrupt changes indicate that the computation of q^0 and R probably was not completely stable, although k_r-values were computed now, instead of estimated. Results by Kouwenhoven (1994) show a similar non-smooth behaviour. At the start of the experiment, R-values for basin M08 even reached negative values. Obviously, $q^0 \cdot F(I)$
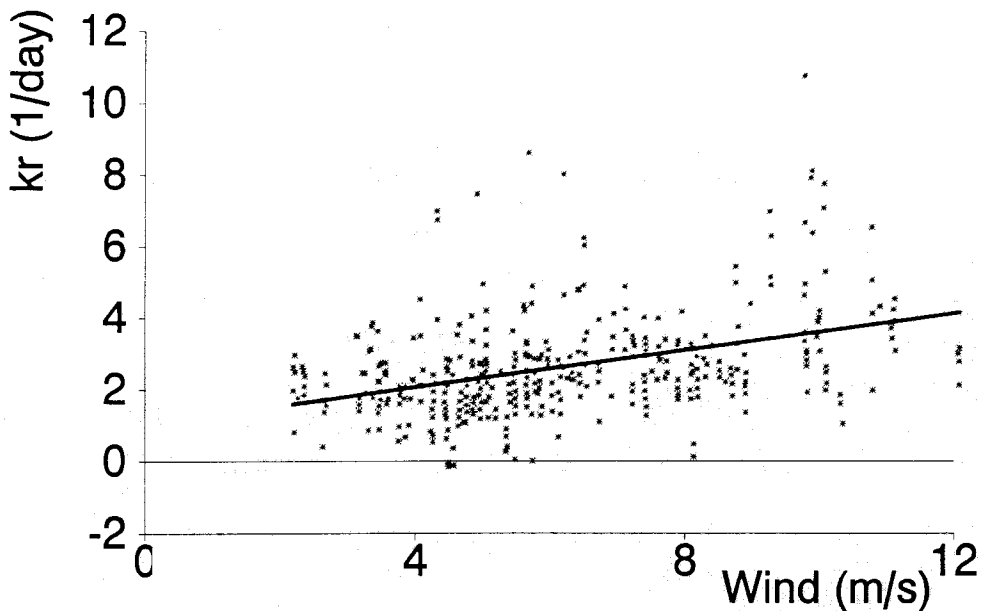

Fig. 3. Relationship between estimated (after equation 9) k_r-values and daily averaged wind speed (KNMI, 1992). Regression line represents equation (17)

Fig. 2. I: Result of STEM-analysis for day 100 in 1992, basin M08. $k_r = 0.729$ d^{-1}, R $= 2.28$ (mg O$_2 \cdot$ l$^{-1} \cdot$d^{-1}), q $= 0.0272$ (mg O$_2 \cdot$ l$^{-1} \cdot$d$^{-1} \cdot$(W$\cdot$m^{-2})$^{-1}$). 1 (line): simulated oxygen concentration, 2 (squares): measurements, 3(dots): oxygen saturation values.
II: Approximately 90 % parameter uncertainty contours for 6 datapoints and 3 parameters (n = 6, p = 3 in equation 13) for day 100 STEM-results, basin M08. 1: k_r and R, 2: k_r and q, 3: q and R. Estimates of k_r, q and R are given as dots
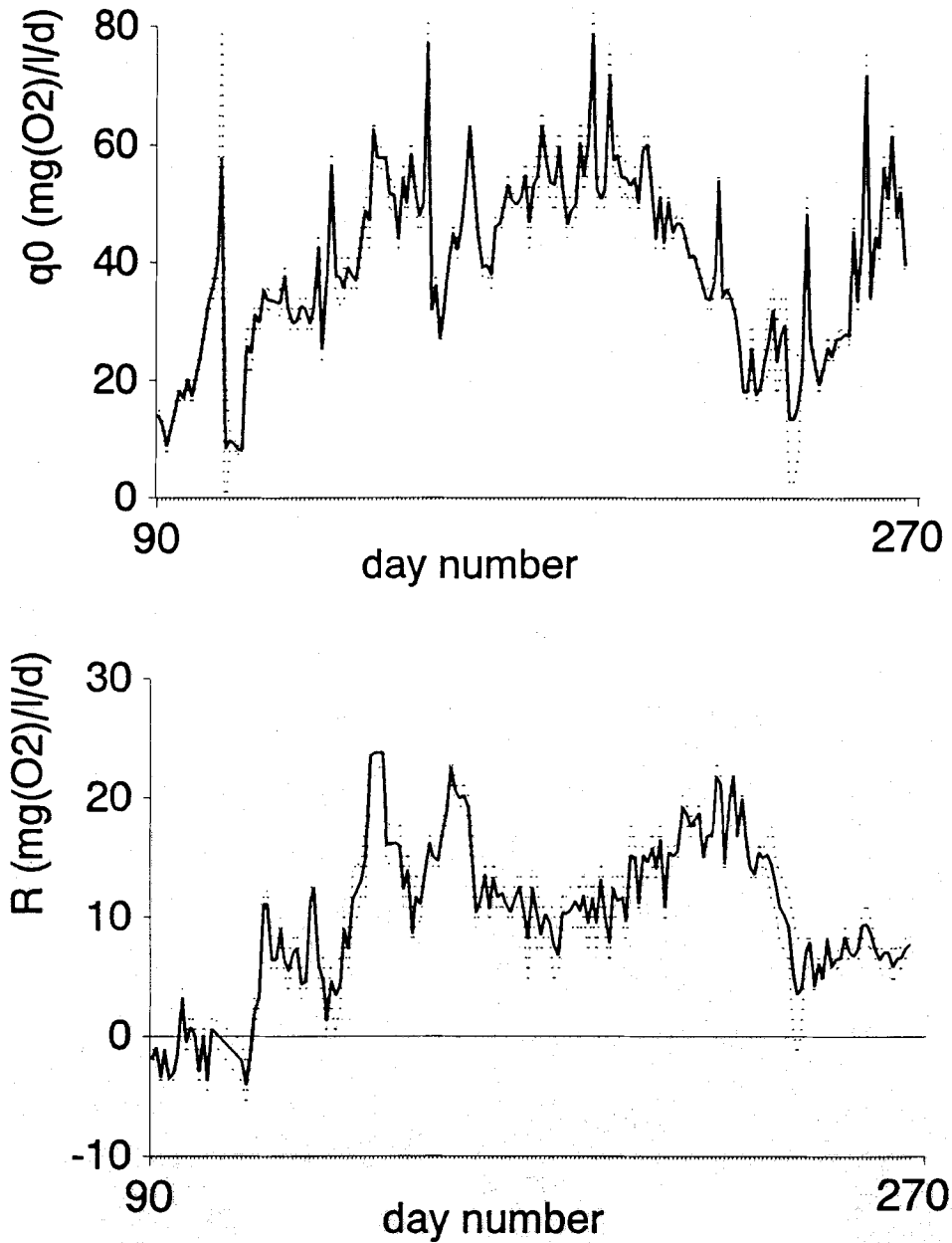
Fig. 4. Daily estimates (after equation 9) q^0 and R for basin M08 during 1992, including an estimate of their individual 90 % reliability (Holtrop, 1993)
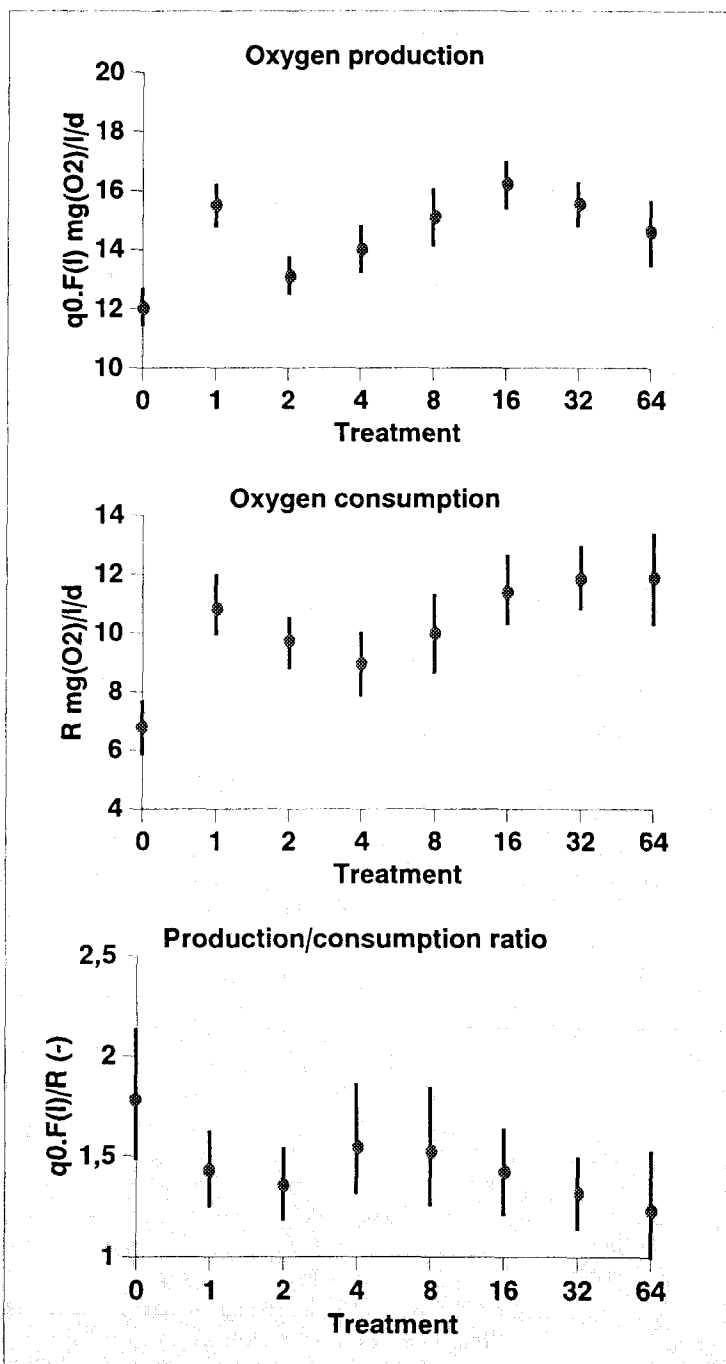
Fig. 5. Estimated production $q^0 \cdot F(I)$ (equation 15), R-values (both in mg $O_2 \cdot l^{-1} \cdot d^{-1}$) for all basins, and estimated production/consumption ratio = $q^0 \cdot F(I)/R$ related to the treatment of each basin

could not account for the oxygen production. Here the computed reaeration might be too high (negative contribution to C(t)). However, the same analysis including estimated reaeration (not shown) also resulted in negative R-values.

Because of such irregularities, it was decided to average all the 180 daily production ($q^0 \cdot F$ (I) and consumption (R) values. All these values are depicted in Figure 5, for each of the eight basins. The production/consumption ratios are also shown. Neither consumption nor production changed very much with increasing nutrient loads. The different nutrient loads are very weakly reflected by the dynamic responses of the experimental systems. The production/consumption ratio decreased somewhat with increasing loads, indicating that at higher loads consumption became more important. Kouwenhoven (1994) analysed several natural systems and found production/consumption ratios of roughly 1.0.

DISCUSSION

The most important conclusion is that it generally seems possible to derive activity parameters for oxygen consumption and production from the dissolved oxygen time-series. However, one should be very careful in assigning strict values to the results: parameter uncertainties should always be known. The parameter values show how the dynamics of the system change during the season, and how they differ from basin to basin, thus reflecting the effect of the treatment. As a result of such an analysis, system characteristics are derived that would otherwise not be available. Thus, the method as presented here extends the knowledge of the ecological system; it allows a better interpretation of other biotic and abiotic data.

The production-radiation relationship was kept very simple in our analysis. The introduction of a photosynthetic parameter through equation (14) gave better results in terms of a lower sum-of-squares, but the value of I_k was not very well investigated; it is possible to make improvements. Equation (14) with $I_k = 400$ ($W \cdot m^{-2}$) implies that there is some photosynthetic saturation. However, a translation to biological parameters needs a description of the underwater light climate (see e.g. Golterman, 1975), which is beyond the scope of this paper.

For all basins, $q^0 \cdot F(I) \cdot R^{-1} > 1.0$ (Figure 5). This may be a result of

– the experiment mainly being carried out during the growing season (storage of organic matter); the period of mineralization is not completely covered.

– outflow of produced matter; observations indicated that such an outflow occurred. The biotic data that were sampled indicated that organic matter storage probably was of minor importance compared to flushing.

– a structural error in the computation of k_r. The oxygen concentrations were generally above the saturation level because the experiment was carried out during the growing season. This implies that reaeration was a loss term in the oxygen budget, similar to R. A structural error in k_r would cause a structural error in R.

In this paper, data-analysis was restricted to the oxygen time-series. During the research, more biotic and abiotic variables were monitored. Since the q^0- and R-parameter values reflect the activities of the organisms, the linking of these parameter values with biotic and abiotic observations would increase the value of the present analysis, and vice versa. Brinkman et al. (1994) describe such an analysis to estimate the separate contribution of

the three major groups of primary producers in the system. The result is quite hopeful, although it proved to be difficult to find a clear relationship between each contribution and the nutrient treatment.

The authors feel that further progress may be possible after the introduction of a more detailed description of biotic and abiotic processes. However, a problem would then be that not all the process descriptions can be separately calibrated. All the applied parameters were estimated in the present analysis. After the first complete analysis, we decided to compute the reaeration parameter, but the applied relationship was not known in advance. In an extended model, such a complete parameter estimation would not be possible anymore. This implies that a priori information has to be added to such extended models. Finally, integrated ecosystem models with many detailed descriptions of biotic and abiotic processes may also be applied to the mesocosm results (e.g. Brinkman et al., 1991). In that case, an important goal may not only be system analysis, but also the testing of the adequacy of such an ecosystem model. Model ecosystem results as described in the present paper have to be extrapolated to 'real' systems, for which ecosystem models and their more simple precursors may be, in our opinion, very useful. System analysis as presented here may enhance the applicability of ecosystem models and model ecosystems in understanding large systems.

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