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MESOCOSMS AND ECOSYSTEM MODELLING

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MODÉLISATION
DYNAMIQUE DE L'OXYGÈNE
ANALYSE DE SYSTÈME
MÉSOCOSMES
PRODUCTION PRIMAIRE
CONSOMMATION D'OXYGÈNE
ENSOLEILLEMENT

RESUME – Une modélisation dynamique utilisant différents niveaux d'agrégation est appliquée au résultat d'une expérience en mésocosme reproduisant les effets de l'enrichissement en nutriments sur les variables caractéristiques du système (composition et biomasse algale, zooplancton et zoobenthos). Un modèle de la dynamique de l'oxygène correspondant à un haut niveau d'agrégation a été employé pour analyser une série temporelle de mesures d'oxygène. Ensuite, un modèle de production primaire (niveau moyen d'agrégation) a été appliqué à ces données d'oxygène augmentées de données biologiques. Les modèles à forte agrégation aussi bien que les modèles d'écosystèmes sont utiles pour étudier le comportement de mésocosmes. Le choix du modèle et du niveau d'agrégation dépendent de la question spécifique posée. Les modèles à forte agrégation donnent une estimation des paramètres les plus fiables, tandis qu'une agrégation faible permet une meilleure analyse des processus de l'écosystème.

MODELLING
OXYGEN DYNAMICS
SYSTEM ANALYSIS
MESOCOSMS
PRIMARY PRODUCTION
OXYGEN CONSUMPTION
REAERATION
INSOLATION

ABSTRACT – Dynamic model analysis at two different levels of aggregation was applied to the results of a mesocosm experiment on the effects of nutrient loading on coastal benthic ecosystems. An oxygen dynamics model with a high level of aggregation was first used to analyze oxygen time series. The productivity estimates of the first model were then linked with additional biotic and abiotic data to estimate the separate contributions of three groups of primary producers to the total production. Highly aggregated models as well as more detailed models proved to be useful to study ecosystem behaviour in mesocosms. The choice of the model depends on the specific question addressed. Models with high aggregation levels supply more reliable parameter estimates, while low aggregation models lead to better insight in ecosystem processes.

INTRODUCTION

Many tools and methods are available to study ecosystems and ecosystem processes. They vary from large scale ecosystem studies in the field to studies on single species in the laboratory. Mesocosms are considered to be the link between these two extremes. Medium scaled experimental enclosures integrate many processes, but are possible to control, at least to a certain extent. Generally, mesocosms are not suited to study processes at a species level, although species can be monitored accurately. The results resemble reality more than laboratory experiments do, due to the more natural behaviour of organisms (Brock *et al.*, 1993). However, system behaviour cannot be predicted absolutely, because certain field conditions may be suppressed in mesocosms, e.g. the effects of wind.

The system behaviour in mesocosms is generally studied by monitoring chemical and biological state variables in the system, such as phosphorus concentration, algal cell counts, zooplankton densities 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 analyzed using (multiple) regression analysis techniques and non-deterministic models such as time-related polynomes (Roberts, 1992). However, these methods generally fail to describe the dynamic interrelations that are active in the system. In addition to the state variables, one has to pay attention to the underlying processes 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.*, 1991 ; Oviatt, 1986 ; Sampou & Oviatt, 1991 ; Sullivan *et al.*, 1991).

The system behaviour in the mesocosm can be subsequently described by using models which include both data on state variables and on processes. The models applied may differ in the degree of aggregation and the degree of integration. A model with a high level of integration incorporates all processes which are thought to be important, and thus describes the entire ecosystem. Models with a low level of integration are restricted to sub-processes such as air/water exchange, sediment oxygen demand and benthic primary production. Models with a high aggregation level lump many processes, whereas models with low levels of aggregation describe processes in more detail. Consequently, an ecosystem model which covers the entire ecosystem and describes processes in detail is considered to be a model with a high level of integration and a low level of aggregation.

Outdoor marine mesocosm facilities were constructed on the island of Texel to study shallow estuarine ecosystems, such as the Wadden Sea. These experimental ecosystems are used to examine the responses of such ecosystems to changes in environmental conditions. In 1990, the project BEST (Benthic Eutrophication Studies) was set up to study the response of coastal benthic systems to eutrophication, with special emphasis on the hypertrophic situation in the Venice Lagoon in Italy. Fieldwork in the Venice Lagoon itself was supported by experimental work in mesocosms at Texel. The mesocosms were installed to closely resemble a relatively unpolluted situation in the Venice Lagoon. During this experiment, several state variables and processes were regularly measured in all mesocosms, at least once every 5 weeks. In addition, oxygen concentrations were

measured at a very high frequency, viz. every 30 seconds. The oxygen time series may be analyzed by using models that describe the relevant processes of changes in oxygen concentration and their effects at the different levels of aggregation (Van Straten, 1986 ; Van Straten & Kouwenhoven, 1991 ; Keesman, 1989).

This paper describes the results of the analysis of the oxygen concentration time series, using two models with a similar high level of integration but with a different level of aggregation. Finally, the application of these models for mesocosm studies are discussed in relation to their predictive power.

MATERIAL AND METHODS

Mesocosms

Eight 21 m² basins, 0.5 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). The basins were flushed continuously with Wadden Sea water, the residence time of the water was one week. The response of the mesocosm ecosystems to the different nutrient additions was monitored from March to September 1992. Oxygen, insolation and water temperature were measured every 30 seconds, and 15 minutes averages of these samples were recorded (Fig. 2). The main biological and chemical variables of the ecosystem and the additional supply water were monitored at regular intervals ranging from 1 to 5 weeks, viz. nutrient concentrations in the water and sediment, light attenuation coefficients, biomass and species composition of the phytoplankton, microphytobenthos, macroalgae, zooplankton and zoobenthos, and the production, respiration and nutrient fluxes.

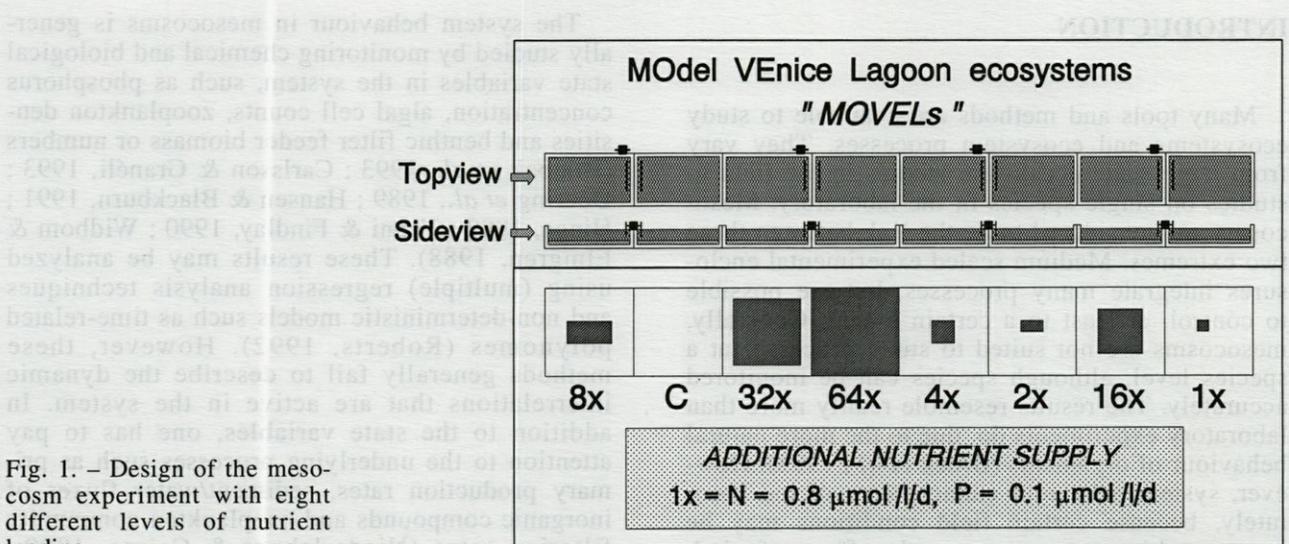


Fig. 1. – Design of the mesocosm experiment with eight different levels of nutrient loading.

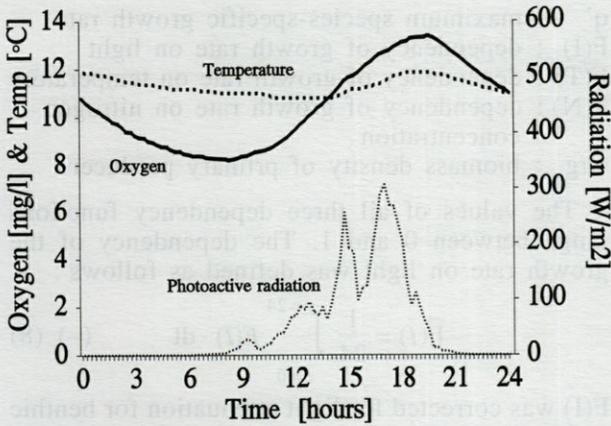


Fig. 2. Dissolved oxygen concentration ($\text{mgO}_2 \cdot \text{l}^{-1}$), global radiation ($\text{W} \cdot \text{m}^{-2}$) and water temperature ($^{\circ}\text{C}$) in MOVELOO at daynumber 122 in 1992.

Model analysis

Model 1 : Analysis of oxygen dynamics

The first model which was used to analyze the oxygen time series (Fig. 3), was characterized by a high level of aggregation. The single aim of this analysis was to estimate general system characteristics, viz. total oxygen production and total consumption rates. The basic processes which were included in this oxygen dynamics model are primary production, oxygen consumption and reaeration, i.e. oxygen exchange between atmosphere and water (Fig. 3). Since all processes are lumped into these three groups, the model results give virtually no information on the underlying processes. Such a model is therefore only valid if the underlying processes or variables do not significantly change during the experimental period.

Primary production is a species-dependent function of several environmental conditions such as light, temperature and nutrient concentrations. It was assumed that light is the only control variable that changes during a period of 24 hours. Therefore the primary production reads :

$$\text{Production} = q \cdot I_0 \quad (\text{mg}(\text{O}_2) \cdot \text{l}^{-1} \cdot \text{d}^{-1}) \quad (1)$$

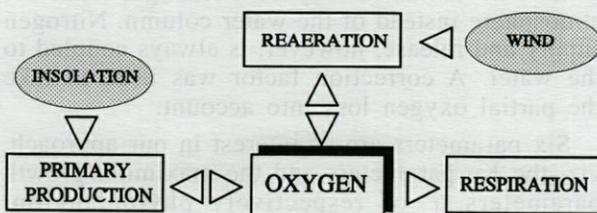


Fig. 3. - Scheme of model I.

where I_0 is the global radiation, expressed as $\text{W} \cdot \text{m}^{-2}$. The photosynthetic parameter q ($\text{mg}(\text{O}_2) \cdot \text{l}^{-1} \cdot \text{day}^{-1} \cdot (\text{W} \cdot \text{m}^{-2})^{-1}$) consequently lumps all the remaining relationships, e.g. temperature, nutrient concentrations and light attenuation in the water column.

Consumption includes the degradation of organic matter (detritus) by pelagic and benthic bacteria, and the respiration by primary producers and pelagic and benthic fauna. The consumption rate R reads :

$$\text{Consumption} = R \quad (\text{mg}(\text{O}_2) \cdot \text{l}^{-1} \cdot \text{d}^{-1}) \quad (2)$$

Reaeration depends, amongst other factors, on temperature, salinity and oxygen saturation concentration in the water :

$$\text{Reaeration} = k_r \cdot [C_{\infty}(T, \text{Sal}) - C_t] \quad (\text{mg}(\text{O}_2) \cdot \text{l}^{-1} \cdot \text{d}^{-1}) \quad (3)$$

where k_r is the reaeration coefficient (day^{-1}), and C_{∞} is the oxygen saturation concentration in the water. The temperature (T) and salinity (Sal) dependency of C_{∞} was taken into account. The coefficient k_r itself is also temperature dependent, but the variation with temperature is much smaller than that of C_{∞} .

Combining the three basic groups of processes, the oxygen dynamics model reads :

$$\frac{dC}{dt} = q \cdot I_0 - R + k_r \cdot [C_{\infty}(T, \text{Sal}) - C] \quad (\text{mg}(\text{O}_2) \cdot \text{l}^{-1} \cdot \text{d}^{-1}) \quad (4)$$

The input and output of matter was not included in this analysis, since the residence time of the water exceeded the period of each analysis.

The values of the parameters q , R and k_r could subsequently be estimated from the oxygen time series. The differential equation (4) was solved by means of two methods : (1) by simulating $C(t)$ and (2) from data-point (t) to data-point ($t + 1$).

When simulating $C(t)$, only the starting value $C(0)$ was thought to be known, or may be estimated. After the simulation, the set of measured values of the oxygen concentration $C(t)$ was compared with the set of estimated values $C_i(t)$.

By the second method, the differential equation (4) was solved from data-point (t) to data-point ($t + 1$) :

$$C_{i,t+1} = (1 - \Delta t \cdot k_r) \cdot C_t + \Delta t \cdot q \cdot I_{0,t} + \Delta t \cdot k_r \cdot C_{\infty,t} - \Delta t \cdot R \quad (5)$$

where $C(t)$ is the measurement at time t . Thus, each measurement $C(t)$ was a new starting point for the computation of $C_{i,t}(t + 1)$. It was assumed that T , Sal and I were continuous and could be differentiated at $[t, t + \Delta t]$.

Parameters values for both methods were obtained by minimizing the sum of squares S of residues R_i :

$$S = \sum_{i=1}^m R_i^2 = \sum_{i=1}^m (\hat{C}_i - C_i)^2 \quad (6)$$

for all m observations, where \hat{C}_i was the computed oxygen concentration and C_i the measurement. The simulation and subsequent parameter estimation according to the first method was performed by means of the STEM software package (ReMeDy, 1991). This program uses a Nelder-Mead (Simplex) minimization procedure which is robust, but not very fast. Application of the second solving method, which was done using the Matlab scientific software tools (MATLAB, 1991), usually results in smaller residues than when solving the equation according to the first method, because estimations are started with the measured situation at $t = t$ for each separate time interval $[t, t + \Delta t]$.

When applying a model, errors principally occur in the data, in the model, and in the parameters. The errors in the data appeared to be of minor importance (Zuur, 1993). The errors in the model may be found by examining the structure of R_i of equation (6). In general, a regular (non-white noise) structure of the residues R_i implies that at least one important factor was not, or not correctly, described by the model. Errors in parameters may be due to interchangeability: parameters are highly interchangeable when the same quality of the simulation results is found when using different combinations of parameter values. In such cases, the data are insufficient to discriminate between the several processes that are incorporated in the model. Uncertainty analysis was applied in order to examine errors in parameters (Draper & Smith, 1981).

Model II : analysis with incorporation of biotic data

The second model used to analyze mesocosm data was characterized by a lower level of aggregation than the first model. Here the productivity estimates were linked with additional data in order to estimate the contributions of the primary producers in the mesocosms to the total production. The primary producers were divided into three groups, viz. benthic microalgae (benthic diatoms), pelagic microalgae (diatoms and flagellates) and pelagic macroalgae (Enteromorpha and Ulva). The oxygen production of each group of primary producers reads:

$$\text{Production} = q' \cdot \bar{F}(\bar{I}) \cdot F(T) \cdot F(N) \cdot \text{Org} \\ (\text{mg}(\text{O}_2) \cdot \text{l}^{-1} \cdot \text{d}^{-1}) \quad (7)$$

- q' : maximum species-specific growth rate
- $F(I)$: dependency of growth rate on light
- $F(T)$: dependency of growth rate on temperature
- $F(N)$: dependency of growth rate on nitrogen concentration
- Org : biomass density of primary producer

The values of all three dependency functions range between 0 and 1. The dependency of the growth rate on light was defined as follows:

$$\bar{F}(\bar{I}) = \frac{1}{24} \int_{t=0}^{t=24} F(I) \cdot dt \quad (-) \quad (8)$$

$F(I)$ was corrected for light attenuation for benthic and pelagic production. The sum of the oxygen production of the three groups of primary producers should be equal to $q \cdot F(I_0)$ as was defined in equation (1).

Additionally, a nitrogen budget was included into the computations:

$$\frac{dN}{dt} = -\gamma_N \cdot [\text{Production} - \text{Respiration}] + \text{Flux} + \\ + \text{Inp} - \text{Outp} + \text{Addit} \\ (\text{mg}(\text{N}) \cdot \text{l}^{-1} \cdot \text{d}^{-1}) \quad (9)$$

- Inp, Outp : natural inflow and outflow of nitrogen ($\text{mg} \cdot \text{l}^{-1} \cdot \text{d}^{-1}$).
- Addit : amount of nitrogen added to the basin ($\text{mg}(\text{N}) \cdot \text{l}^{-1} \cdot \text{d}^{-1}$).
- Flux : contribution due to sediment/water exchange ($\text{mg}(\text{N}) \cdot \text{l}^{-1} \cdot \text{d}^{-1}$).
- Y_N : N/O ratio in all algae ($\text{g}(\text{N})/\text{g}(\text{O}_2)$).

The amount of nitrogen added to the basins and the natural inflow of nitrogen was measured, and the outflow of nitrogen was calculated from the actual nitrogen concentration in each basin and the water outflow. The remaining relationship to be described was the dependency on N-availability. This was done according to a classical Monod-equation:

$$F(N) = \frac{N}{(K_N + [N])} \quad (-) \quad (10)$$

where K_N is the Monod-parameter.

The reaeration coefficient (eq. 3) was reduced in proportion to the coverage of the water surface by macroalgae. Macroalgae produce and use oxygen, some of which may be exchanged with the atmosphere instead of the water column. Nitrogen supply and release, however, is always coupled to the water. A correction factor was used to take the partial oxygen loss into account.

Six parameters are of interest in our approach, viz. the K_N parameters and the maximum growth parameters q' of respectively phytoplankton, microphytobenthos and macroalgae. It was impossible to estimate all six parameters because

the K_N values and the production rate parameters appeared to be highly interchangeable. This was mainly due to the limited number of biomass measurements. We assumed therefore that K_N equalled $14 \mu\text{g} \cdot \text{l}^{-1}$ for all three primary producers (De Vries *et al.*, 1988).

The primary production was coupled to the actual N-concentration through the above-mentioned Monod-function. However, N-data were too variable, which corrupted the estimation of q' -values. In order to improve the estimation, N-concentrations were estimated by setting $dN/dt = 0$ in eq. (9), and computing the necessary [N]. Subsequently, the difference between measured and computed [N]-values were minimized according to eq. (6). Thus, not only the q values from section I, but also the measured [N]-values were used in the minimization computation. The minimization target F reads.

$$F = \sum (q - q'F(T) \cdot F(N) \cdot \text{Org})^2 + \beta_N \cdot \sum ([N]_{\text{meas}} - [N]_{\text{comp}})^2 \quad (11)$$

with β_N as a weighting factor.

RESULTS

Model I

Comparison of the measured and calculated oxygen concentrations reveals that the calculated oxygen concentrations were lower than the measured concentrations in the morning hours, and higher than the measured concentration in the afternoon hours (Fig. 4). This difference may be due to an underestimation of production and/or an overestimation of consumption during the morning, or vice versa.

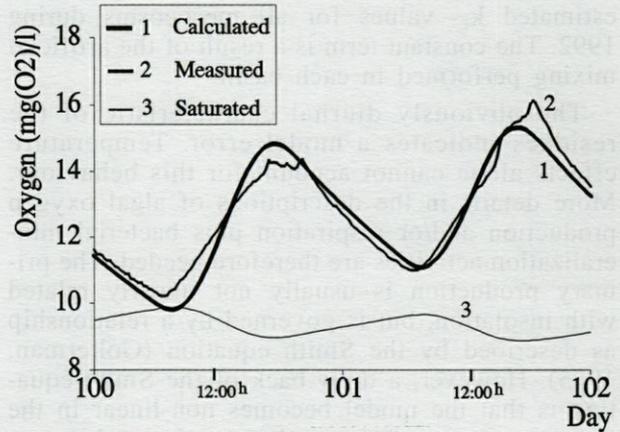


Fig. 4. – Measured, calculated and saturated dissolved oxygen concentration ($\text{mgO}_2 \cdot \text{l}^{-1}$) in MOVELO0 at from daynumber 100 to 102 in 1992, as estimated by the original model I by simulating $C(t)$.

Although the individual confidence intervals of the parameter estimates q , R and k_r are rather small, the combined 90 % confidence contours of parameter estimates allow a much larger deviation from the best estimates (Fig. 5).

Especially the reaeration coefficient k_r and the consumption rate R show a strong interchangeability. Since the k_r -parameter is mainly dependent on the wind velocity, the parameter exchangeability between k_r and R was eliminated by computing instead of estimating k_r . All daily reaeration coefficients were assumed to be related to wind velocity according to

$$k_r = \frac{1}{\text{depth}} \cdot \{0.517 + 0.129 \cdot U_{wi}\} \quad (\text{d}^{-1}) \quad (12)$$

where U_{wi} was the wind speed ($\text{m} \cdot \text{s}^{-1}$) at 10 m (KNMI, 1992). Equation (12) was based on all

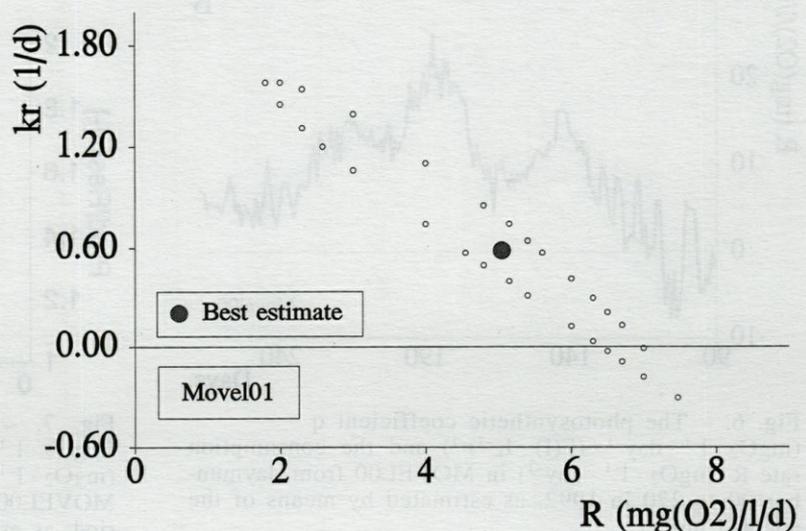


Fig. 5. – Confidence intervals (90 %) and best estimates of parameter combination of the consumption rate R ($\text{mgO}_2 \cdot \text{l}^{-1} \cdot \text{day}^{-1}$) and the reaeration coefficient K_r ($\text{mgO}_2 \cdot \text{l}^{-1} \cdot \text{day}^{-1}$) as estimated by means of the original model I. Day 122, Movel 01.

estimated k_r -values for all mesocosms during 1992. The constant term is a result of the artificial mixing performed in each basin.

The obviously diurnal characteristic of the residues indicates a model error. Temperature effects alone cannot account for this behaviour. More details in the descriptions of algal oxygen production and/or respiration plus bacterial mineralization activities are therefore needed. The primary production is usually not linearly related with insolation, but is governed by a relationship as described by the Smith equation (Golterman, 1975). However, a draw-back of the Smith-equation is that the model becomes non-linear in the Smith-parameter. The non-linear relationship was therefore approximated by means of the linear relation :

$$F(I_z) = \begin{cases} \frac{I}{I_k} & ; I < I_k \\ 1.0 & ; I > I_k \end{cases} \quad (-) \quad (13)$$

where I_k ($W \cdot m^{-2}$) was the photosynthetic parameter.

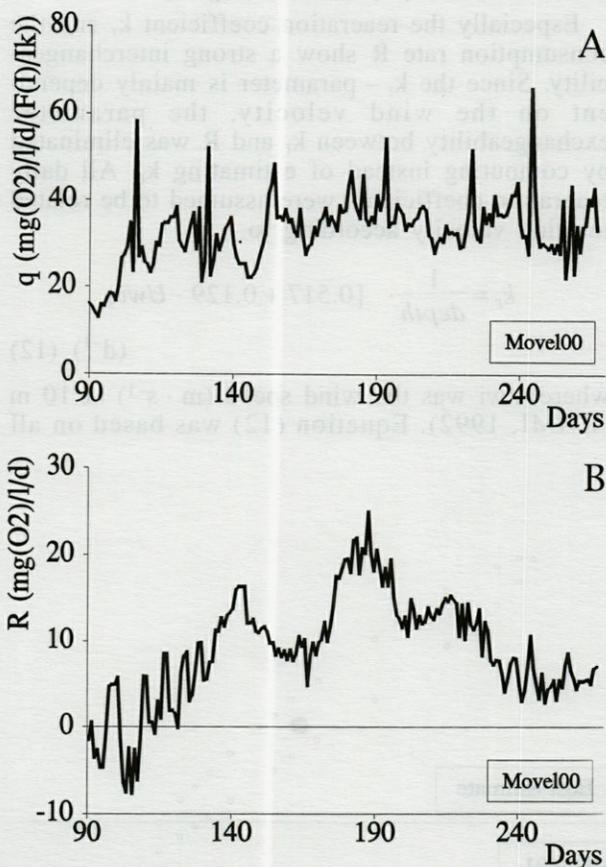


Fig. 6. - The photosynthetic coefficient q ($mgO_2 \cdot l^{-1} \cdot day^{-1} \cdot (F(I) \cdot I_k^{-1})^{-1}$) and the consumption rate R ($mgO_2 \cdot l^{-1} \cdot day^{-1}$) in MOVel00 from daynumber 90 to 270 in 1992, as estimated by means of the adapted model.

These two adaptations to the original model resulted in better parameter estimates. When the residues of the original and adapted model were compared, both after eq. (5), the adaption not only led to smaller residues, but also to a more white characteristic of this noise.

As an example, the values of the photosynthetic coefficient q and the consumption rate R for MOVel00 (reference basin) during the entire research period in 1992 are shown in Fig. 6.

The average production rate as well as the average respiration rate seem to increase with increasing nutrient loading (Fig. 7). The ratio

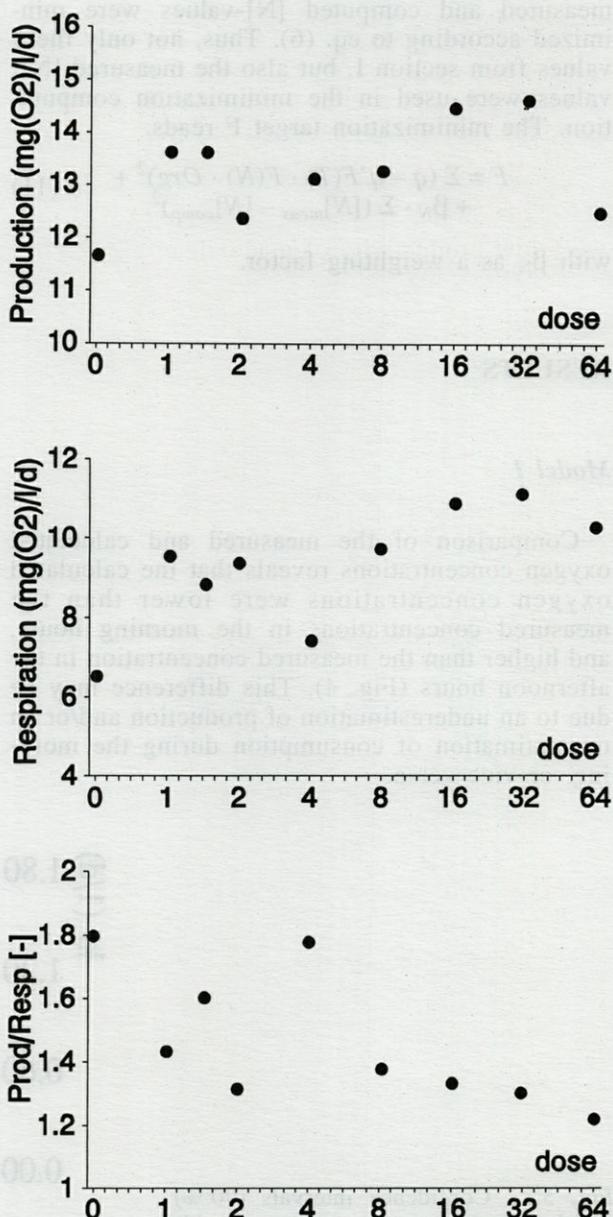


Fig. 7. - The average photosynthetic coefficient q ($mgO_2 \cdot l^{-1} \cdot day^{-1}$), the average consumption rate R ($mgO_2 \cdot l^{-1} \cdot day^{-1}$) and the ratio between q and R in MOVel00 to MOVel64 for the entire experimental period, as estimated by means of the adapted model I.

(production/respiration) decreased with increasing loading.

Model II

Assuming that the Monod constants K_N equalled $14 \mu\text{g} \cdot \text{l}^{-1}$ for all three groups of primary producers, the photosynthetic coefficient q ($q' \cdot F(T) \cdot F(N) \cdot F(\text{shade}) \cdot [\text{Org}]$) as estimated by means of model II seems to be reasonably related to the photosynthetic coefficient q (oxygen model), as estimated by means of the adapted model I (Fig. 8).

The estimates for the maximum growth parameters of phytoplankton, microphytobenthos and macroalgae respectively, were 17.72, 9.66 and 0.29 d^{-1} . The subsequent calculation of the average primary production of each group of algae during the experimental period showed that microphytobenthos was the main producer of oxygen in most mesocosm ecosystems (Fig. 9). The relatively low productivity of macroalgae of 0.29 d^{-1} was compensated by their large biomass. This, in contrary to phytoplankton, which combined high productivity with low biomass. The average production of phytoplankton, microphytobenthos and macroalgae was not clearly related to the nutrient loading.

CONCLUSIONS

This paper shows that it is possible to derive information on ecosystem behaviour from oxygen time series by means of a dynamic oxygen model

with a high level of aggregation. The results of model I analysis showed that the values of the photosynthetic coefficient q and the consumption rate R varied during the experimental period and that they were related to the additional nutrient supply. The model with a medium aggregation level, model II, revealed additional information on the contribution of the primary producers to the values of the photosynthetic coefficient q .

Finally, ecosystem models with a low aggregation level may be used to estimate parameters of more detailed processes in the mesocosm ecosystems, e.g. flows of matter, fluxes and process rates. These parameter estimates may be subsequently tested for the effects of the treatment and results may be used to estimate mass budgets for the mesocosm ecosystem.

However, several drawbacks appear when lowering the level of aggregation. Even in mesocosms, not all state variables and processes which are necessary for parameter estimation can be measured, or can be measured frequently enough. Part of his problem may be solved by using data from literature, or employing "best guesses". In addition, individual parameter uncertainties generally increase with a decrease in aggregation level. Therefore, ecosystem models with low levels of aggregation may be used to estimate ecosystem parameters, but one should be very careful in assigning strict values to the results and always be aware of parameter uncertainties.

Highly aggregated models, as well as ecosystem models, are useful to study the behaviour of mesocosm ecosystems, extending the knowledge of the system and allowing the interpolation and a better interpretation of the biotic and abiotic data. The predictive power of models with a high

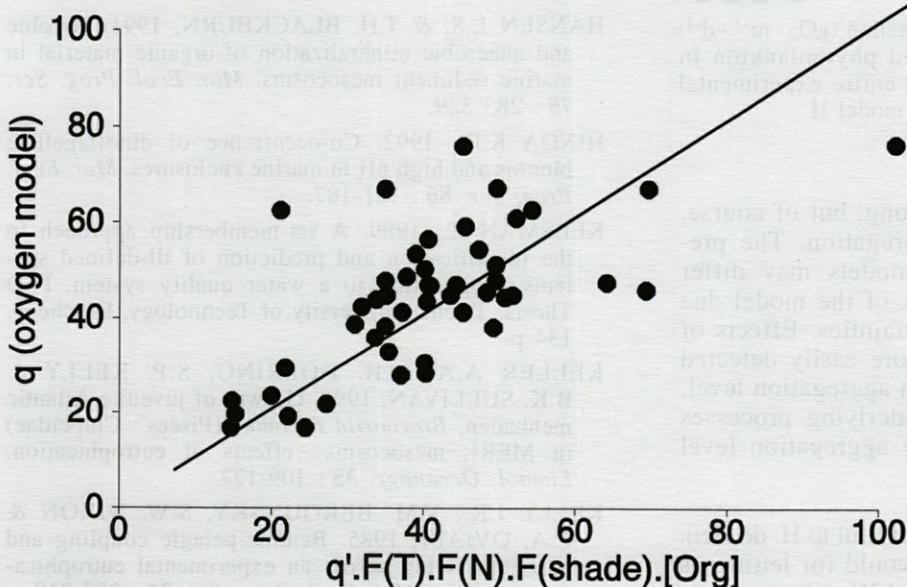


Fig. 8. - The relationship between the photosynthetic coefficient q ($q' \cdot F(T) \cdot F(N) \cdot F(\text{shade}) \cdot [\text{Org}]$) as estimated by means of model II and the photosynthetic coefficient q (oxygen model) as estimated by means of the adapted model I.

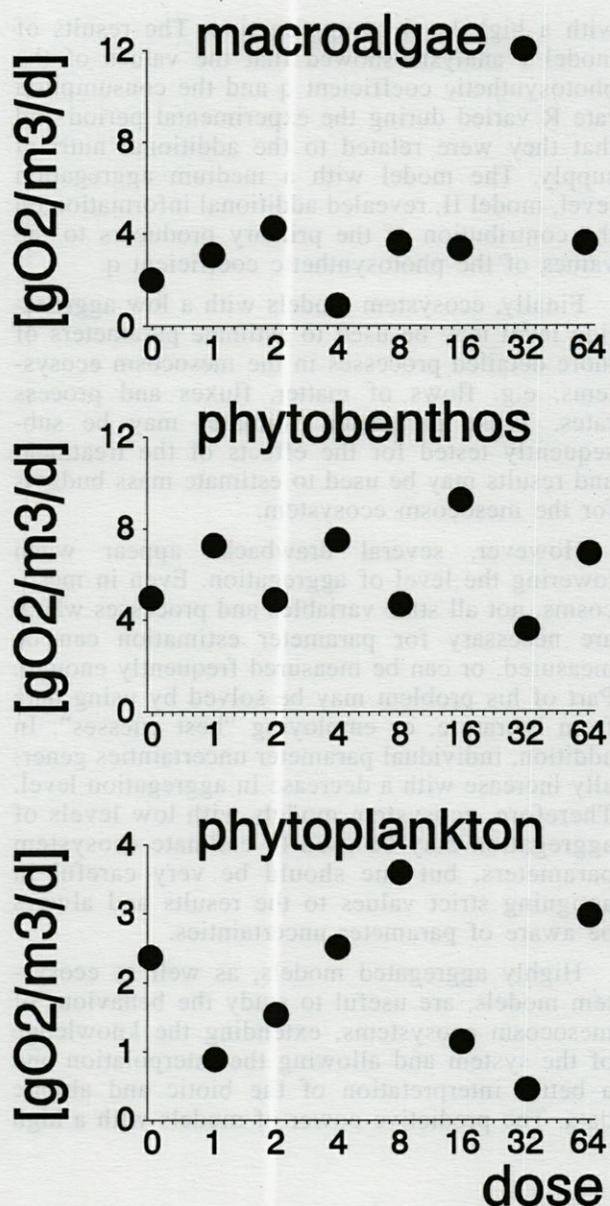


Fig. 9. – The average primary production ($\text{gO}_2 \cdot \text{m}^{-3} \cdot \text{d}^{-1}$) of macroalgae, phytobenthos and phytoplankton in MOVELO0 to MOVELO64 for the entire experimental period, as estimated by means of model II.

level of aggregation can be strong, but of course, only at the same level of aggregation. The predictive power of ecosystem models may differ substantially for different parts of the model due to differences in relative uncertainties. Effects of treatments will therefore be more easily detected by means of models with a high aggregation level. If more detailed insight in underlying processes is required, application of low aggregation level models should be favoured.

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