Linear understanding of a huge aquatic ecosystem model using group-collecting sensitivity analysis

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Abstract

Huge complex ecosystem models with several hundred parameters and large input data sets escape standard attempts at integral assessment. We introduce the concept of group-collecting sensitivity analysis in which related model parameters or forcing coefficients are combined into subsets. Since means and standard deviations of subsets are varied instead of individual coefficients, the method is numerically efficient and produces a condensed amount of results. Application to the Aquatic Ecosystem Model (AQEM) is presented. AQEM is a descendant of the European Regional Seas Ecosystem Model (ERSEM) with a finer process and spatial resolution with respect to the Wadden Sea. A two-dimensional sub-structured sensitivity table, which is the major result of this approach, enables an immediate perception of sensitive functional relationships and dependencies between individual parameters and the relevant characteristics of a near-shore aquatic ecosystem. Special emphasis is placed on differences in average and seasonal behaviour. The response of selected result variables to the variations of the majority of group parameters is correlated, i.e. result variables show a similar sensitivity to variations in a specific parameter group. We show that exceptions to this rule lead to a deeper insight into the model system.

Key words: sensitivity analysis, ERSEM, North Sea, Wadden Sea, aquatic ecosystem model, model evaluation

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1 Introduction

Complex ecological models simulate the dynamics of a wide range of output variables. Descriptions of physical processes are typically interwoven in various kinds of biological models, sometimes extended by chemical formulations. This kind of integration is addressed by models describing various different systems, e.g. aquatic ecosystems (Lancelot et al., 2000), terrestrial ecosystems in general (Friend et al., 1997) or forests and individual tree dynamics (Köhler, 2000; Bugmann, 2001). For such purpose a large array of input parameters is necessary. Most of these parameters represent specific process coefficients which can only be measured with difficulty. The uncertainties of parametrisation as well as the nonlinearity of interactions within the model lead to two main questions. Do the model dynamics react sensitively to changes of individual (uncertain) parameter values? If so, which parameters or corresponding processes, respectively, have the most influence on specific output variables? Answering the first question indicates which parameter values might need further evaluation and where modifications should be applied to gain more robust model results. Moreover, tackling the second question is central to our understanding of the simulated system. It leads to a tentative ranking of effective modes in the system and is of interest for a wide range of model applications, such as the planning of a large integrated field study (Klepper et al., 1994). An extensive analysis stage is, furthermore, central to model development, adaptation or reduction (Snowling and Kramer, 2001). This is especially true if simulation tools usable for decision support have to be built on the basis of complex environmental models (Wirtz, 2001).

Sensitivity Analysis (SA) is a process which aims to assess the contribution of input parameters to uncertainties in the model output. To address the two questions stated above as generally as possible, we will perform a SA allowing us to determine the effect of most – if not all – input parameters on selected output variables. With the standard "one-factor-at-a-time" method (OAT) the impact on specific goal variables of changing one parameter at the time is determined (Daniel, 1973; Morris, 1991). The OAT approach, however, yields a sensitivity matrix with numerous columns or rows when applied to complex models. In this situation, Klepper (1997) proposed a cluster analysis of the result matrix. We found that a post-processed SA, though resolving the problem of data overflow, is hardly interpretable in terms of key system processes. Hence we here suggest a pre-processing method which before variation combines related parameters into groups.

The object of our analysis is the Aquatic Ecosystem Model (AQEM, Ebenhöh, 1996). AQEM incorporates more than 3000 individual parameter values and is largely identical with the European Regional Seas Ecosystem Model (ERSEM, Baretta-Bekker, 1995; Baretta-Bekker and Baretta, 1997). ERSEM describes the main processes within the complex food web of the the North Sea ecosystem, including pelagic and benthic organisms and nutrient cycles. As a refinement with respect to ERSEM, AQEM spatially focuses on the Wadden Sea, and in particular on the tidal inlet of Spiekeroog Island. This area was of special interest during the large integrated project "Ecosystem Research of the Lower Saxonian Wadden Sea" from 1992 to 1997 (Dittmann, 1999). Its aims was to evaluate stability properties of the system as well as anthropogenic changes such as eutrophication. Not surprisingly, these aims largely shaped the specific design and goal variables of the group-collecting SA shown in this study.

Starting in 2001, ecosystem processes in the back-barrier tidal inlet of Spiekeroog are being investigated by the Research Group "Biogeochemistry of the Wadden Sea". Since field research has to be confined to a limited number of observables, we also aim at a theoretically based ranking of processes or variables in relation to their relevance for biogeochemical cycling in coastal waters and sediments.

2 Short description of AQEM

In in the first implementation of ERSEM (Baretta-Bekker, 1995), the North Sea is divided into ten homogeneous boxes of different size. Boxes which cover areas deeper than 30 m are further subdivided into an upper and a lower part (Fig. 1). Advective transport between the boxes are described using a data–base derived from independent hydrodynamic modelling (Lenhart et al., 1995; Radach and Lenhart, 1995). Boundary conditions prescribe seasonally varying inputs of nutrients from the atmosphere, rivers and neighbouring areas (e.g. English Channel). Extending the spatial domain of ERSEM I, AQEM covers eight additional boxes representing the back-barrier tidal inlet of Spiekeroog Island (Fig. 1). Altogether, the biogeochemical cycles of C, O, P, Si and N–species are accounted for. Simulated micro-scale physical mechanisms include light attenuation by suspended particulate material as well as the sinking of senescent phytoplankton. The whole model is forced by daily–averaged incident radiation, depending on cloud cover and day length.

The biological constituents of the model are organised into functional groups in both the benthic and the pelagic sub–model. The functional groups are described according to the concept of 'standard organism' (Baretta et al., 1995). Within this concept universal biological processes such as food uptake, assimilation, respiration, excretion, predation or mortality and the related nutrient and carbon fluxes are considered. Three classes of standard organism are distinguished: primary producers, consumers and decomposer. Each of these classes contains different functional groups of species (e.g. diatoms and picophytoplankton are functional groups within the class of primary pro-

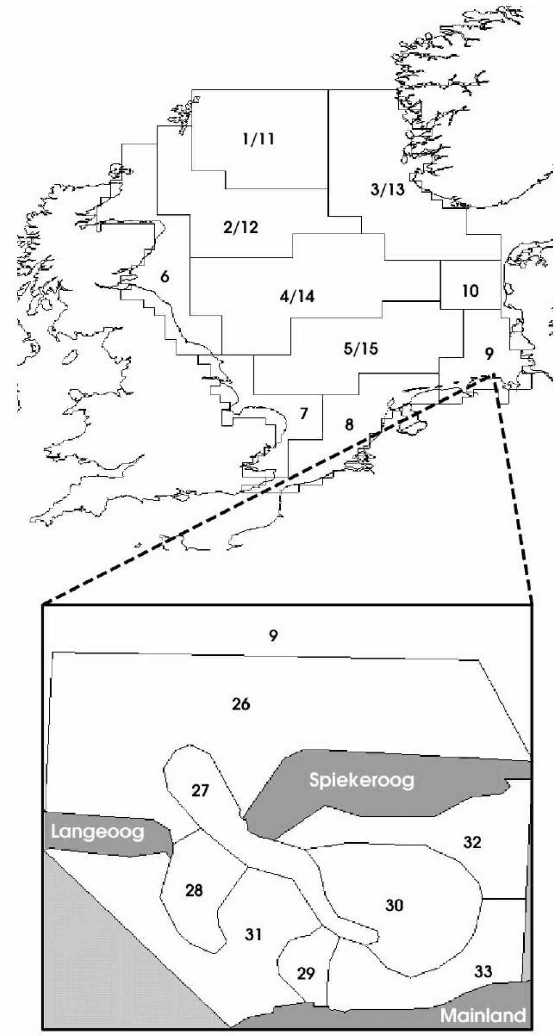

Figure 1. AQEM box resolution of the North Sea and the Wadden Sea. The deep boxes are divided into an upper part of 30 m depth (boxes 1 to 5) and a lower one from 30 m down to the bottom (boxes 11 to 15). The fine scale spatial division of the Wadden Sea in the back-barrier tidal inlet of Spiekeroog Island contains 8 monolayer boxes. The small transport to adjacent tidal inlets (light gray areas) is neglected.

ducers). Differences between functional groups in the same class are observed in experiments and then realised in different parameter values in the model. An example of fluxes and processes considered in the model is shown for the standard organism of a consumer or secondary producer (Fig. 2). The food web of all represented functional groups is found in Fig. 3. For a complete description, see the fully published Ersem documentation (Baretta-Bekker, 1995; Baretta-Bekker and Baretta, 1997).

Aqem or Ersem, respectively, also resolves a microbial food web where dissolved forms of organic carbon (excretion products) are converted into par-

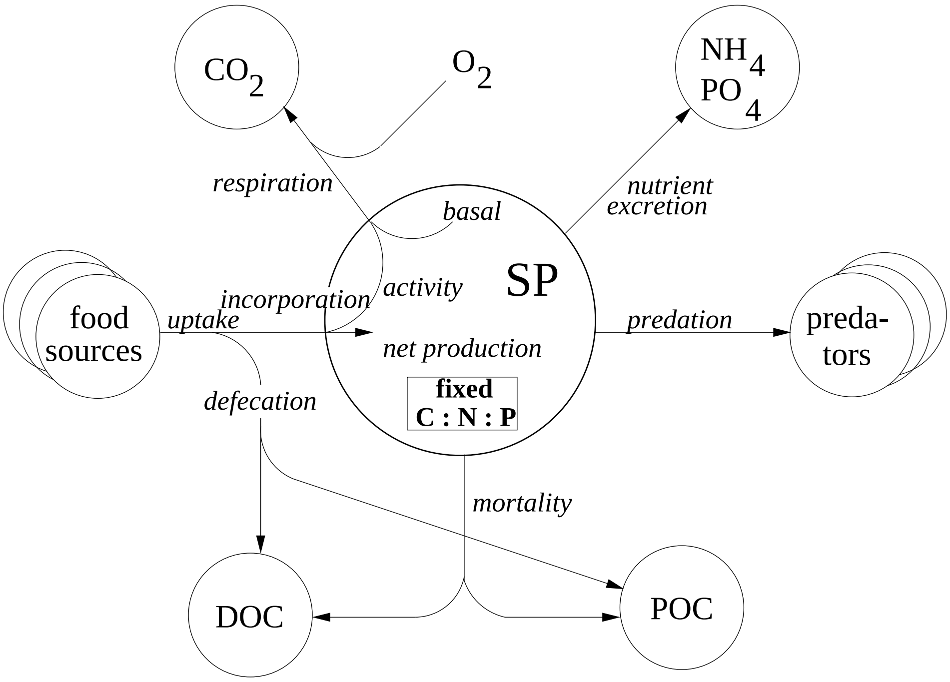

Figure 2. The concept of standard organisms applied to benthic and secondary pelagic producers (SP). Different processes and the fluxes of nutrients and carbon are illustrated.

ticulate forms. All functional groups contribute to the detritus pools by lysis, egestion, sloppy feeding and mortality. The benthic sub-model contains a food web model describing carbon and associated nutrient cycles, and a bioturbation/bioirrigation module to calculate the diffusive transport of dissolved substances and the vertical transport of particulate matter in the sediment in relation to the presence and activity of the benthic biota. Furthermore, changes of vertical positions of the oxygen and sulphide horizons and a range of nutrient fluxes are described.

Because of the shallowness of the area of interest (average depths between 1.3 m and 8.3 m), additional processes have to be considered. Thus, the transport of particulate detritus, the light adaptation of phytoplankton and the near-coastal transport of particulate matter are improved (Ebenhöh, 1996).

The conceptual time-step of the model is one day, but diurnal and tidal cycles are implicitly resolved. The numerical time-step is always smaller than the conceptual one.

The standard parameter set used here was defined and tested in previous studies and publications (Baretta-Bekker, 1995; Ebenhöh, 1996).

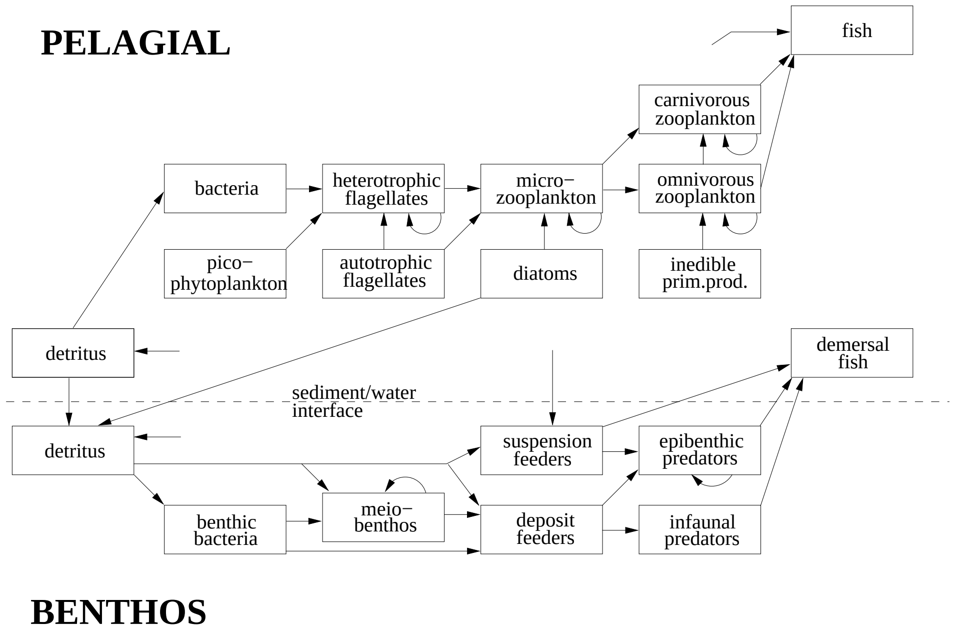

Figure 3. The pelagic and the benthic model food web. The detritus fraction and the benthic bacteria are not subdivided as in the model. Less important feeding links are not indicated. Arrows without a specific starting point indicate multiple inputs which are not visualised in the Figure.

3 Group-collecting sensitivity analysis

3.1 Definition of parameter groups

The two questions proposed in the introduction can most simply be addressed via a systematic sensitivity analysis by which variations of single parameters are studied according their effect on specific output variables. However, due to the large number of input values the standard OAT variation leads to excessive computation times as well as severe difficulties in visualising the results comprehensively. Hence, for our study we combine related single members of parameters p_i into groups $P_j \equiv P$, where the index j is omitted in order to simplify the notation. For the AQEM parameter set, the definition of parameter groups can be realised by two collecting conditions. First, a group is defined by equivalent interaction coefficients of different functional groups in the same class, e.g. Michaelis–Menten constants for nutrient–limited growth of all autotrophs (diatoms, flagellates, etc.). Second, we combine monthly values of boundary conditions, e.g. mean nitrogen inflows of the River Rhine at 12 times of a long-term averaged year. In the following, a variation always refers to the variation of an individual group P instead of an individual parameter. In this way, the total amount of required variations is reduced by a factor 1/9 (from 3188 single parameters to 350 parameter groups). To preserve the effect of different sensitivities within one group, we introduce two types of group variations. So let $\overline{p}$ be the average value of the single parameter values p_i of one parameter group P.

Within the first variation (M), the influence of changing the global mean $\overline{p}$ is investigated, whereas the deviation of individual parameter values from $\overline{p}$ is changed during a second variation (D). The latter method provides insights into the importance of the variability within one group. In detail, we have for both approaches:

- Variation M: Every single parameter is
(1) increased by 50% of the average value ($p_{i,M1} = p_i + 0.5 \cdot \overline{p}$),
(2) decreased by 50% of the average value ($p_{i,M2} = p_i - 0.5 \cdot \overline{p}$).
- Variation D: Every single parameter is
(1) set to a value whose difference from the average $\overline{p}$ is doubled ($p_{i,D1} = p_i + (p_i - \overline{p})$),
(2) set to the average value ($p_{i,D2} = \overline{p}$).

Taking half the mean $\overline{p}$ as perturbation in variation M provides a meaningful estimate of the confidence interval as well as inter-specific variations within each group, much more reliable than referring to each p_i separately. A major pre-condition for this approach is the similar physical or biological meaning of all p_i within a group.

3.2 Sensitivity index

Let R be a strictly positive result variable of interest, its value in a simulation with standard parametrisation R_0 and its value after changing the parameter group P to P_X be $R(X)$ ($X = M1, M2, D1, D2$). We define the sensitivity index $S_X(R)$ of R with regard to the variation X of P by

$$S_X(R) = \left|1 - \frac{R(X1)}{R_0}\right| + \left|1 - \frac{R(X2)}{R_0}\right|, \qquad X = M, D. \tag{1}$$

Thus, total insensitivity of R with regard to variation X would give a sensitivity index $S_X(R) = 0$. High sensitivity, e.g. a 50% change in R_0 in $X1$ and $X2$ yields $S_X(R) = 1$. Due to the summation of absolute outcomes of the up- and down-variation, non-linearity as such is not measured. Because the variation M and D follow different patterns, the two sensitivity indices $S_M(R)$ and $S_D(R)$ are not directly comparable. The definition of our sensitivity index S (Eq. 1) is not universal. Other definitions which for instance take the differences from the varied parameter values to the standard values into account (Morris, 1991) or which estimate effects of two-factor interactions

Table 1
Description of selected result variables

Symbol	Description
SWI-C	Shannon-Wiener-Diversity index of total C-fluxes
PO_4	Concentration of phosphate (pelagic)
Si	Concentration of silicate (pelagic)
NH_4	Concentration of ammonium (pelagic)
NO_3	Concentration of nitrate (pelagic)
Chlorophyll-A	Chlorophyll-A content of phytoplankton
Zoobenthos	Biomass of zoobenthos
Zooplankton	Biomass of zooplankton
Pelagic bacteria	Biomass of pelagic bacteria
Aerobic bacteria	Biomass of aerobic benthic bacteria
Anaerobic bacteria	Biomass of anaerobic benthic bacteria
Diatoms vs. other phytoplankton	Biomass ratio of diatoms to other algal species groups

(Campolongo and Braddock, 1999), are possible.

3.3 Variables of interest

The choice of result variables R is obviously case-specific. In principle, few but meaningful variables should be chosen and, if possible, several variables of interest should be combined into integral measures. Analysing many result variables might reduce the comprehensibility of the sensitivity analysis.

Table 1 summarises the result variables used in this study. A main issue for which AQEM was derived from ERSEM and which it has to resolve was the effect of eutrophication on the carbon dynamics of the Wadden Sea ecosystem. To characterise the simulated nutrient cycles we choose to monitor the biomass of functional groups incorporated in AQEM such as phytoplankton, zooplankton, zoobenthos and bacteria. Furthermore, concentrations of pelagic

Table 2
Overview of varied parameter groups. The origin, the number of parameter groups in a submodul (no), the number of individual values in one parameter group, called dimensions of this group (dim) and the underlying biological and physical processes of the parameter groups are briefly described. Altogether 3188 values of 350 different parameter groups were changed in this sensitivity analysis.

Origin	No	Dim	Details
Biology	99	4, 5	Growth and uptake parameters of bacteria, primary producers, pelagic and benthic secondary producers
Transport	9	1	Transport processes, mainly concerning Wadden Sea and sedimentation
Physics	32	1, 33	Parameter concerning temperature, irradiance for photosynthesis, and other physicochemical processes
Riverine input	166	1, 12	Input concentrations of nine substances (ammonium NH_4), nitrite (NO_2), phosphate (PO_4), silicate (SiO_4), nitrate (NO_3), organic nitrogen (orgN), organic phosphorus (orgP), organic silicate (orgS) and organic carbon (orgC)) from 18 river catchments (Scheldt, Meuse, Rhine, West Lyssel, East Lyssel, Ijmuiden, Ems, Weser, Elbe, Tyne & Tees, Humber, Thames, Jade, Schleswig-Holstein, Denmark, Firth of Forth, Lauer, and Yzer)
Atmospheric input	1	12	Input concentration of atmospheric nitrate (NO_3)
External input	43	1, 12	Input concentration of four substances (phosphate (PO_4), nitrate (NO_3), silicate (SiO_4), and ammonium (NH_4)) from 10 different boundary areas (Norway (upper & lower), Shetland (upper & lower), Fair Isles (upper & lower), Pentland Firth, Baltic Sea (upper & lower), and English Channel)

macro nutrients like PO_4, Si, NO_3 and NH_4 are of interest in this study. The varying species composition of the phytoplankton may be expressed by the biomass ratio of diatoms to other algae. In addition, we define a characteristic quantifying the system behaviour over the whole range of different trophic levels. The Shannon-Wiener Index (SWI-C) of diversity is an initial attempt of such a variable (e.g. Begon et al., 1990). It is applied to all carbon fluxes in the model (Eq. 2).

$$\mathrm{SWI–C} = -\sum_{i=1}^{S} \frac{f_i}{F} \ln\left(\frac{f_i}{F}\right), \qquad (2)$$

with S: number of carbon fluxes, f_i: magnitude of the ith carbon flux, F: sum of all carbon fluxes.

Simulations are driven by environmental field data collected in 1988 and were run over six years, focusing on middle-term effects of the variations of the last simulated year. Since our analysis is focused on the Wadden Sea, the result variables are spatially averaged over the boxes covering the back-barrier tidal inlet of Spiekeroog Island.

Because all result variables show seasonal behaviour, a simple description of $S_X(R)$ needs to be expanded to a depiction covering variability as well as mean values. Thus, the sensitivity is calculated as described in Eq. 1 for both the annual average ($\overline{R}$) and the standard deviation of seasonal values from the average (δR).

The modified analysis is then able to differentiate sensitive behaviour of seasonal fluctuations from changes in annual means. To summarise, four different sensitivity indices $S_X(\overline{R})$, $S_X(\delta R)$ with $X = M, D$ are calculated for each variable of interest.

An overview of the 350 varied parameter groups is given in Table 2, where their general field of origin (e.g. biological process or riverine inputs) is stated. The labels used in the resulting Figs. 4–8 are similar to their names within the simulation program. Short parameter descriptions are incorporated in the figures. For a more detailed explanation of the parameters see the literature cited in the model description.

4 Results

Most (173) of the 210 parameter groups concerning nutrient input concentrations through sea boundaries and rivers did not lead to significant changes in any result variable. Thus, for simplicity's sake, the visualisation of the results

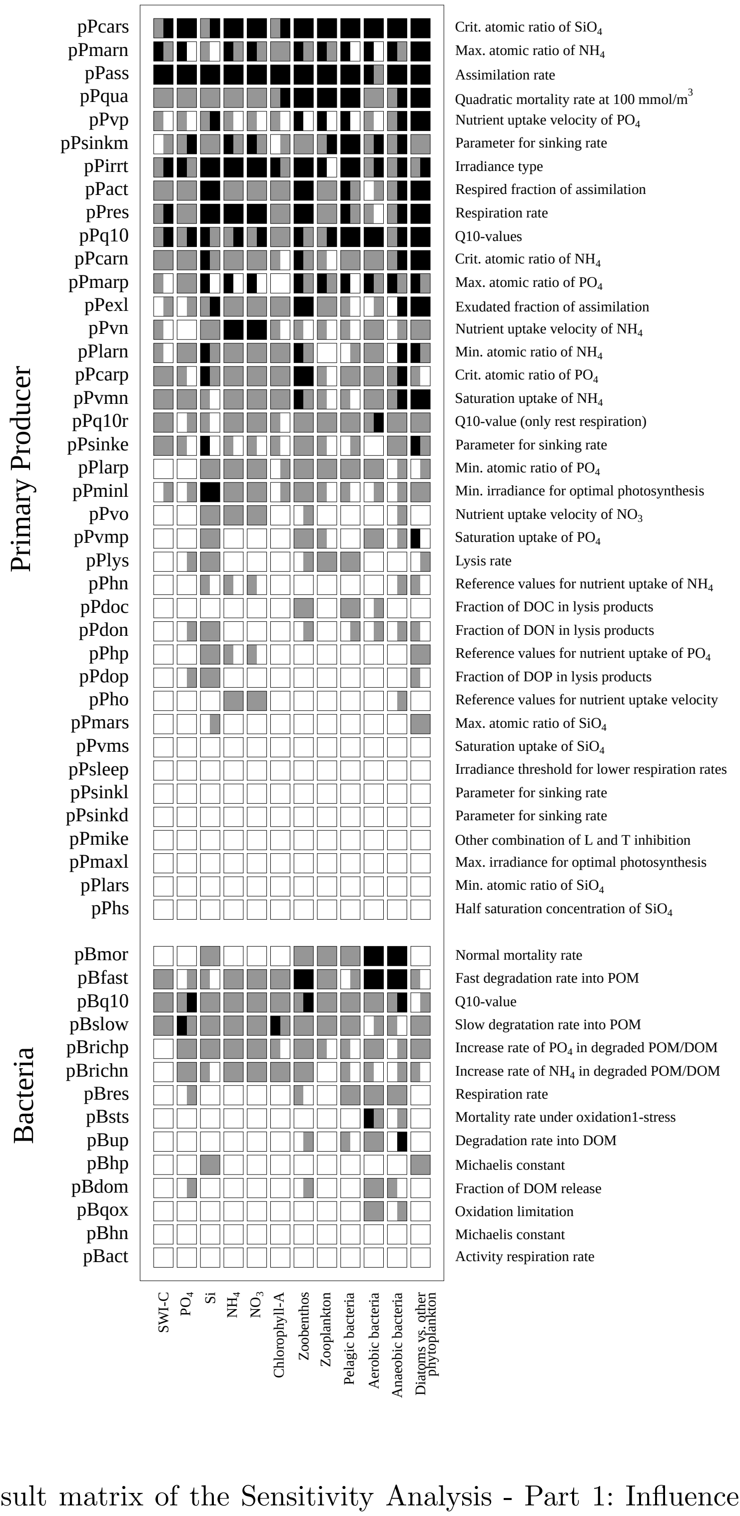

Figure 4. Result matrix of the Sensitivity Analysis - Part 1: Influences of biological parameters concerning primary producers and bacteria. Each subbox contains informations how the result variable reacts on the variation scheme M applied to the respective parameter group. The left half of each subbox covers changes on the yearly averaged values of the results ($S_M(\overline{R})$). In the right half effects on the seasonality in terms of the standard deviation are found ($S_M(\delta R)$). Box filling code: insensitive – white ($S_M < 0.01$); sensitive – grey ($0.01 \leq s_M < 0.1$); highly sensitive – black ($S_M \geq 0.1$).

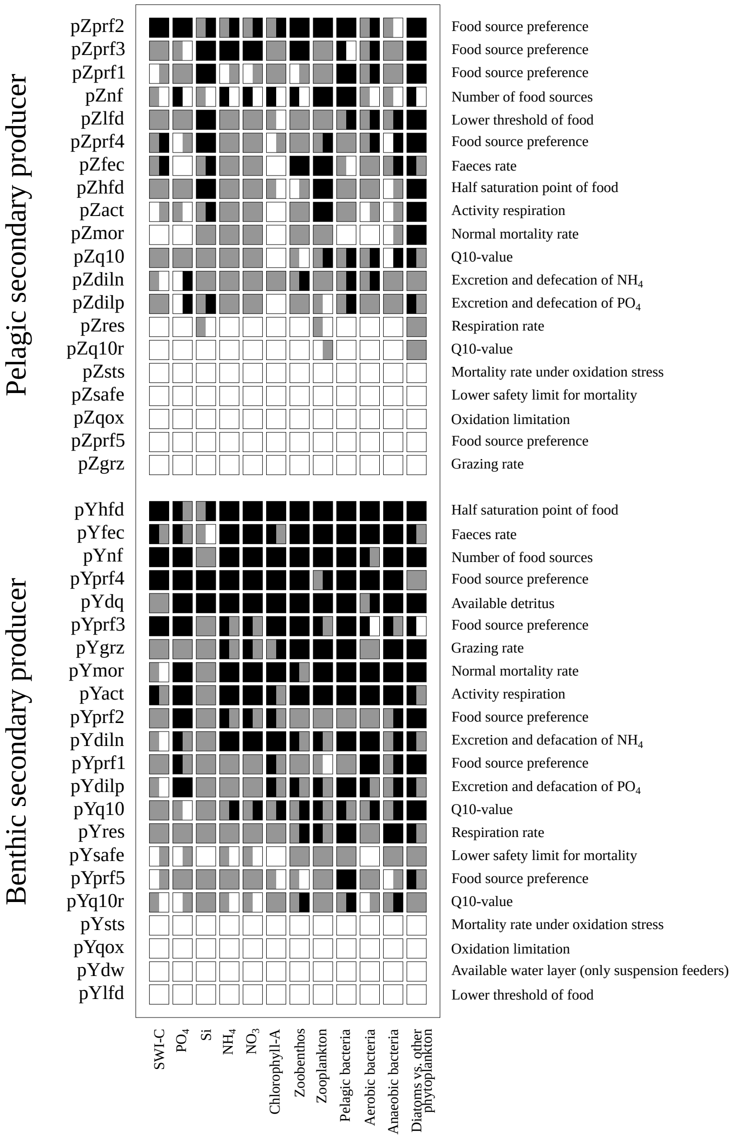

Figure 5. Result matrix of the Sensitivity Analysis - Part 2: Influences of biological parameters concerning pelagic and benthic secondary producers. Each subbox contains informations how the result variable reacts on the variation scheme M applied to the respective parameter group. The left half of each subbox covers changes on the yearly averaged values of the results ($S_M(\overline{R})$). In the right half effects on the seasonality in terms of the standard deviation are found ($S_M(\delta R)$). Box filling code: insensitive – white ($S_M < 0.01$); sensitive – grey ($0.01 \leq s_M < 0.1$); highly sensitive – black ($S_M \geq 0.1$).

of our SA covered all parameters of biological (Fig. 4 and 5), physical and transport origin (Fig. 6), but was restricted to those of effective input origin (Fig. 7). We first restrict the visualisation of results to the indices $S_M(\overline{R})$ and $S_M(\delta R)$.

Surprisingly, none of the four indices generally reached high values (mostly $S <$

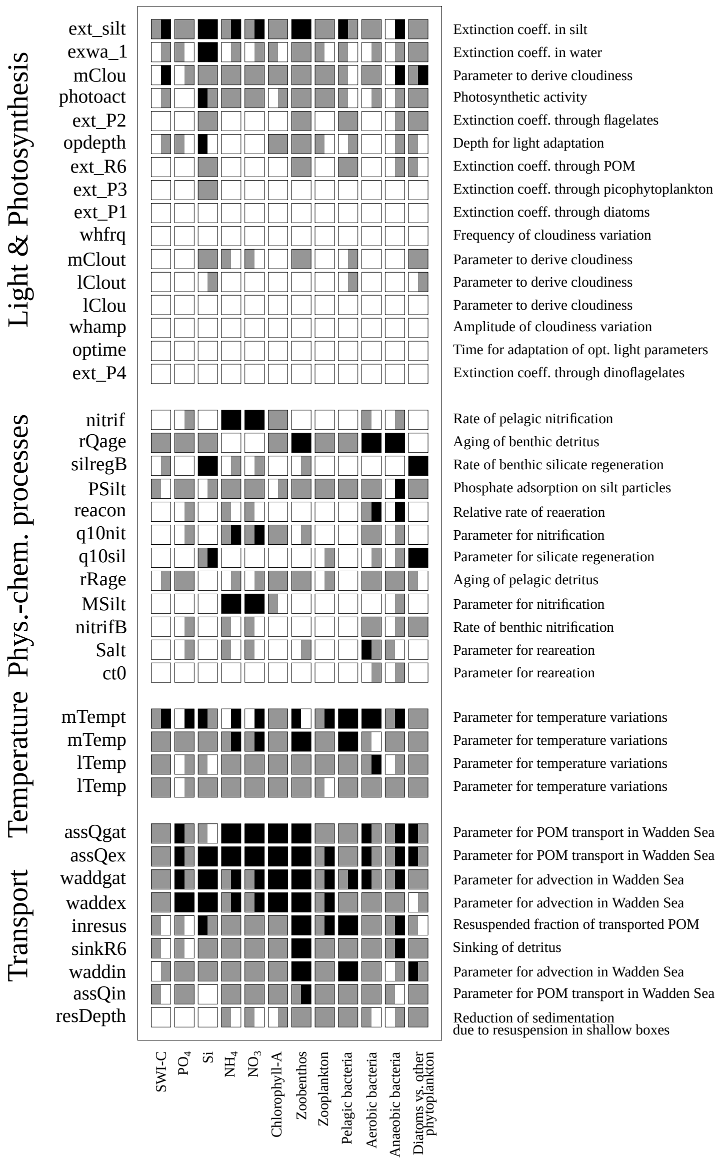

Figure 6. Result matrix of the Sensitivity Analysis - Part 3: Influences of non-biological, mostly physical parameters. Each subbox contains informations how the result variable reacts on the variation scheme M applied to the respective parameter group. The left half of each subbox covers changes on the yearly averaged values of the results ($S_M(\overline{R})$). In the right half effects on the seasonality in terms of the standard deviation are found ($S_M(\delta R)$). Box filling code: insensitive – white ($S_M < 0.01$); sensitive – grey ($0.01 \leq s_M < 0.1$); highly sensitive – black ($S_M \geq 0.1$).

0.5). In this sense the complex ecosystem model can be considered robust. The overall low to intermediate sensitivity values prompted us to distinguish three levels of sensitivity: (i) $S < 0.01$ insensitive; (ii) $0.01 \leq S < 0.1$ sensitive; and (iii) $S \geq 0.1$ highly sensitive. About 26% of the possible 4200 different responses were at least sensitive to the variation M. For the variation D 22% of the responses were sensitive. However, the most highly sensitive answers ($S >$

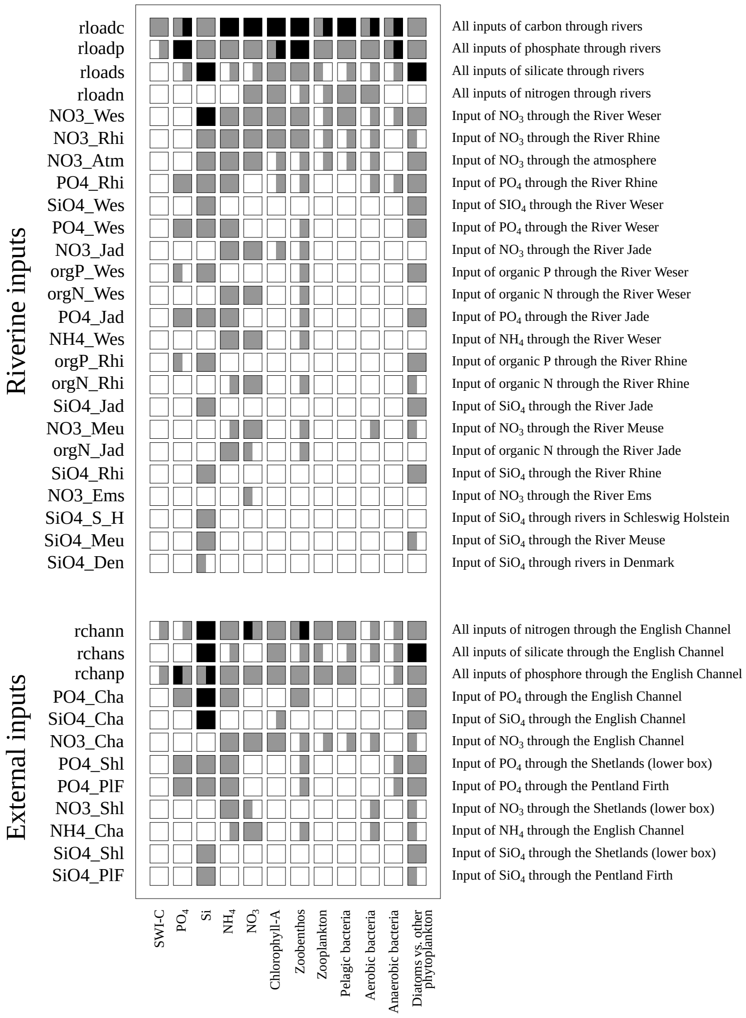

Figure 7. Result matrix of the Sensitivity Analysis - Part 4: Influences of riverine and external inputs. From the 211 different input parameter groups, only the minor part shown led to measurable effects. Each subbox contains informations how the result variable reacts on the variation scheme M applied to the respective parameter group. The left half of each subbox covers changes on the yearly averaged values of the results ($S_M(\overline{R})$). In the right half effects on the seasonality in terms of the standard deviation are found ($S_M(\delta R)$). Box filling code: insensitive – white ($S_M < 0.01$); sensitive – grey ($0.01 \leq s_M < 0.1$); highly sensitive – black ($S_M \geq 0.1$).

0.1) were observed with variation scheme D (16% vs. 9%, Table 3). Despite the different definitions of our four sensitivity indices, they were correlated. Sensitive responses of the result variables occurred similar for different indices S in $46 - 86\%$ of all possible cases. Similar occurrence of highly sensitive results was less frequent ($24 - 86\%$). In detail, we found: (a) a high correlation between the annual average $\overline{R}$ and the seasonal behaviour δR of the same variation scheme, and (b) a correlation between corresponding indices ($\overline{R}$ or δR) of the different variation approaches M or D (Table 3).

Table 3
Individual and similar occurrence of different sensitivity indices. Please note that in this analysis highly sensitive ($S > 0.1$) response was a subset of sensitive ($S > 0.01$) response. The sample size for the individual case was $n = 4200$. For the cases of similar occurrence the sample size n was set to the number of result signals which gained at least one of the two signals investigated for similarity.

Sensitivity index	Sensitive [%] $S > 0.01$	Highly sensitive [%] $S > 0.1$
individual occurrence		
$S_M(\overline{R})$	25.8	8.8
$S_M(\delta R)$	26.6	9.3
$S_D(\overline{R})$	21.5	15.7
$S_D(\delta R)$	22.7	16.3
similar occurrence		
$S_M(\overline{R})$ AND $S_M(\delta R)$	72.3 ($n = 1278$)	52.6 ($n = 498$)
$S_D(\overline{R})$ AND $S_D(\delta R)$	85.5 ($n = 1005$)	86.4 ($n = 721$)
$S_M(\overline{R})$ AND $S_D(\overline{R})$	45.6 ($n = 1369$)	23.5 ($n = 834$)
$S_M(\delta R)$ AND $S_D(\delta R)$	48.5 ($n = 1396$)	26.2 ($n = 851$)

To obtain more detailed links between the sensitivity study to the assessment of ecosystem processes, the parameters were subdivided depending on the sub–module they belong to. This subdivision contained primary producers and bacteria (Fig. 4), benthic secondary producers and pelagic secondary producers (Fig. 5), photosynthesis, other physiochemical processes, temperature and transport (Fig. 6), riverine and external inputs (Fig. 7). Within this subdivision, a ranking of the overall influence of variations in one parameter group P on all selected result variables showed the parameters with the most sensitive responses at the top, those with the most insensitive response on bottom. We found both coefficients whose variations caused insensitive and highly sensitive responses within nearly each parameter array (Figs. 4 – 7). Only the parameters influencing temperature and transport always induced sensitive, if not highly sensitive reactions in the whole set of result variables

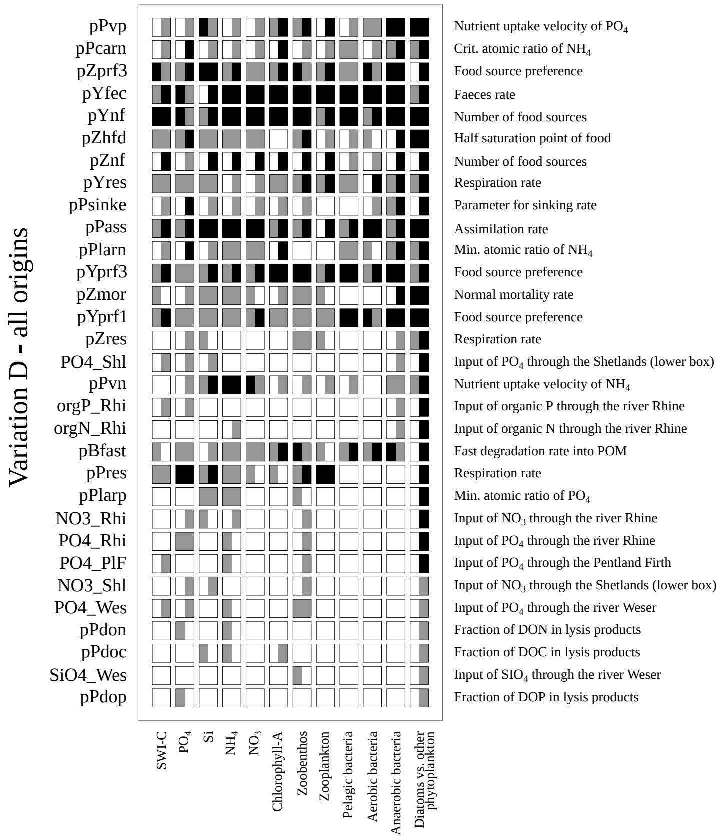

Figure 8. Result matrix of the Sensitivity Analysis - Part 5: Sensitive results of parameters under variation scheme D. Only those parameter groups where both variations $D1$ and $D2$ were performed and which led to at least some sensitive responses are shown. Each subbox contains informations how the result variable reacts on the variation scheme D applied to the respective parameter group. The left half of each subbox covers changes on the yearly averaged values of the results ($S_D(\overline{R})$). In the right half effects on the seasonality in terms of the standard deviation are found ($S_D(\delta R)$). Box filling code: insensitive – white ($S_D < 0.01$); sensitive – grey ($0.01 \leq s_D < 0.1$); highly sensitive – black ($S_D \geq 0.1$).

(Fig. 6). Conversely, 82% of the parameters regulating various input processes at individual locations (rivers, boundaries) did not strongly affect major model outcomes. The most sensitive effects were detected for coefficients controlling all mineral sources simultaneously (rload* in Fig. 7), in particular for carbon and phosphate inputs and for the concentration of NO_3 in the Weser, Rhine and, to a certain degree, the atmosphere.

In the variation scheme D, one-dimensional parameter groups were not varied. Furthermore, in 38% of all cases the variation $D1$ led to parameter values below zero. In these cases the variation $D1$ was omitted and S_D was restricted to the second addend ($S_D(R) = |1 - R(D2)/R_0|$). Thus, the systematic analysis of the importance of parameter group variability was biased towards those P with omitted variations. This shortcoming mainly depended on the degree of differential increase in the scheme $D1$. However, with the chosen doubling of differences between individual values p_i and group averages $\overline{p}$ in only 3 out of 350 parameter groups the values p_i were changed by more than 50% of the averaged value $\overline{p}$ – comparable to the variation intensity in M. Those results in the scheme D not biased by omitted variations led to sensitive responses in just 31 parameter groups (Fig. 8).

To identify the most sensitive of our 12 result variables, the percentages of sensitive and highly sensitive responses were calculated depending on the four different indices (Table 4). The biomass ratio of diatoms to other algal species groups was considerably changed in five out of eight cases followed by the biomass of the zoobenthos. The high variability in the algal community variable is partly caused by its definition since a decreasing non-diatom phytoplankton biomass may lead to pronounced changes here. On the other hand, the Shannon-Wiener Index was most insensitive (6 out of 8). In two cases the PO_4 concentration turned out to be most robust, whereas silicate was the most sensitive nutrient.

Besides these general patterns, we highlight only a few striking relations between individual result variables and varied parameter groups. Especially the simulated seasonal behaviour of aerobic bacteria is susceptible to parameter changes; the same pattern is found for the macrozoobenthos – for both if the dominant coefficients regulating nutrient input are considered (Fig. 7). The seasonality of the ratio of diatoms vs. other phytoplankton was also highly sensitive with regard to the variation scheme D (Fig. 8).

5 Discussion

The sensitivity tables provide a condensed view of the complex interrelations within the modelled ecosystem. In this sense they can be used as look-up tables to identify sensitive responses between input and output variables, depending on the specific questions of interest. While many results lie within *a priori* linear expectations such as the influence of nitrification rates on NO_3 and NH_4, many less trivial results are observed. In particular, unexpected insensitivities such as a missing link between the overall riverine nitrogen input and NH_4 values (rloadn in Fig. 7) yield starting points for further investigations.

Differences among the four indices obtained during the two variation schemes M and D exist but do often not exceed significant levels: the parallel consideration of a number of measures safeguards their interpretation, but is no prerequisite for it. We therefore assume that alternative change and analysis patterns like ones more focused on the nonlinearity of the response, will not yield a much different picture. For example, in our study most of the input processes did not lead to any significant changes or were mostly insensitive to

Table 4
Analysis of sensitivity of chosen results variables (percentages of their sensitive and highly sensitive responses). Please note that in this analysis highly sensitive ($S > 0.1$) response was a subset of sensitive ($S > 0.01$) response. The highest value in each column is set in bold, the lowest value in italics. The description of the result variables is found in Table 1.

Result	Sensitive [%], $S > 0.01$				Highly sensitive [%], $S > 0.1$			
variable	$S_M(\overline{R})$	$S_M(\delta R)$	$S_D(\overline{R})$	$S_D(\delta R)$	$S_M(\overline{R})$	$S_M(\delta R)$	$S_D(\overline{R})$	$S_D(\delta R)$
SWI-C	*18.3*	*19.1*	20.0	*21.7*	*3.4*	*5.1*	*13.4*	*15.1*
PO_4	20.9	24.0	*18.6*	*21.7*	8.0	6.6	14.3	15.4
Si	33.7	30.3	23.4	23.4	10.6	10.6	15.1	16.3
NH_4	30.0	29.1	21.7	23.1	8.3	8.9	15.1	16.0
NO_3	29.7	26.9	21.4	22.6	8.6	8.9	15.1	16.0
Chlorophyll-A	22.9	22.6	22.0	22.9	6.9	6.3	16.9	16.0
Zoobenthos	26.9	**32.6**	22.6	**24.0**	13.4	12.0	16.0	15.4
Zooplankton	25.1	22.3	21.4	*21.7*	7.7	8.3	15.4	15.1
Pelagial bacteria	25.1	24.3	23.1	22.0	10.9	10.3	17.4	16.9
Aerobic bacteria	24.0	28.0	20.3	22.6	7.7	8.9	14.9	17.7
Anaerobic bacteria	18.6	30.3	20.0	23.4	5.7	**15.1**	15.1	17.7
Diatoms vs. other phytoplankton	**34.6**	30.0	**25.1**	23.7	**14.9**	10.3	**19.4**	**18.0**

the variation scheme D. From this we conclude that in the implementation of the model used for this study a monthly resolution of input parameters is of minor importance. This insensitive response to seasonal changes in the forcing might, however, not emerge for other areas like estuaries or lakes. By contrast, those parameters defining temperature are important not only in their averages, but also in their individual values. They clearly belong to first candidates for future monitoring and research as information on temperature dependencies are sparsely found in literature and data-bases.

The high correlation between responses in the averages and standard deviations could imply that our analysis would have been equally detailed if we had restricted the SA to average values. However, this might only be the case for this particular model application.

As stated above, for reasons of computing efficiency the underlying marine ecosystem model (AQEM) uses a spatial division of the North Sea into just 15 boxes. We are aware of the improvements of the spatial resolution into 130 boxes in ERSEM II (Baretta-Bekker and Baretta, 1997). In particular, we expect a better resolved description of nutrient plumes deriving from river discharges adjacent to the Wadden Sea. Therefore we are currently extending the analysis to a new version of AQEM. This version will include finer-scaled hydrodynamic regimes of the North Sea as well as of the Wadden Sea separately calculated for a period of ten years.

When analysing the effect of various input processes it must be borne in mind that our area of interest is restricted to the back-barrier tidal inlet of Spiekeroog Island. Thus, it is not surprising to learn that nutrient discharges of the Rivers Weser and Rhine and the English Channel produce the most intense ecosystem responses (Fig. 7). Compared to a simulation study assessing the Danube influence on the Black Sea food web, the SA presented here shows a slightly different picture. Lancelot et al. (2001) identified phosphate to be the most limiting nutrient, while for the Wadden Sea nitrogen inputs seem to be more relevant.

ERSEM applications to the Adriatic Sea by Zavatarelli et al. (2000) revealed that horizontal and partially also vertical transport are key processes for nutrient and phytoplankton distribution. Our more complete SA substantiates but also differentiates this finding. The total chlorophyll–A amount turns out to be more sensitive to alterations in transport parameters than algal community structure. In AQEM, the latter is dominated by diatoms such that the silicate budget in the tidal inlet gains more importance. With greater water depth compared to the Wadden Sea, the phytoplankton community structure is instead correlated with the nitrogen status of the system (Philippart et al., 2000). Clearly, the dominant role of benthic secondary producers in AQEM is also basically due to the shallow depth of the tidal inlet, tallying with the expectations of field ecologists (Dittmann, 1999). In addition, our SA supports a main result of ERSEM simulations (Vichi et al., 1998) which focus on the cycling of primary producers in a river-dominated area. There, the importance of the inorganic matter concentration or light limitation was emphasised. However, this result is put into another perspective by the sensitive but not highly sensitive outcomes obtained for the array of extinction coefficients in Fig. 6.

The results of our second variation approach D need some further discussion. The bias achieved by omitting some variations is a problem which might always occur in a systematic SA. It is difficult to choose the parameter variations in such ways which avoid values beyond the meaningful range but at the same time cover the interesting spans. The variation intensity used in D was within the range used in our first approach, M, which was found suitable for the modelled system. Furthermore, the fact that 86% of the systematically varied parameter groups only gained insensitive model behaviour with regard to the variation D highlights the stability of the model to interfunctional differences within the biological and seasonal changes within the nutrient subsystems.

To apply our sensitivity analysis to other models one mainly has to adapt the group–collecting criteria to their specific model. Here, we have defined parameter groups either by equivalent interaction coefficients of different functional groups within the same class or by an aggregation of monthly variable boundary conditions to yearly average values. Thus, the approach can easily be applied to other models which work with either the functional grouping concept or time-dependent external forcings. It is very likely that complex models with a huge parameter set are working with the first of the two concepts. The second case is very common for environmental models as these often include high resolution time series of temperature and irradiance. Here the proposed grouping technique can be expected to be highly useful. Even fully coupled hydrodynamics–ecosystem models gain advantage since they (i) depend on many (meteorological) boundary conditions and (ii) need much more computational resources compared to the AQEM application.

To sum up, we have demonstrated that group-collecting SA can be used as a tractable tool to quantify the relative importance of various ecosystem processes or driving forces. One major advantage derives from its completeness including the high number of underlying simulation runs. The ongoing research program “Biogeochemistry of the Wadden Sea” already takes advantage of the obtained parameter ranking when specifying the list of observables to be monitored. Examples include nutrient adsorption on silt particles, aging of detritus, tidal POM transport and highly resolved temperature measurements.

The second benefit of the response patterns will take effect when constructing a reduced ecosystem model starting from the complex one (Wirtz, 2001). To ensure credibility, the systematic approach proposed here is essential since the model structure no longer originates from subjective decisions. We believe an increasing acceptance of simplifications to be a key element of the modelling procedure, especially in the environmental sciences.

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