Environmental Modelling & Software 26 (2011) 124–134

Contents lists available at ScienceDirect

Environmental Modelling & Software

journal homepage: www.elsevier.com/locate/envsoft

Sensitivity analysis for complex ecological models – A new approach

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ARTICLE INFO

Article history:
Received 3 September 2009
Received in revised form
27 June 2010
Accepted 28 June 2010
Available online 17 August 2010

Keywords:
Sensitivity analysis
Global sensitivity
DYRESM–CAEDYM
Lake Kinneret
Ecosystem model

ABSTRACT

A strategy for global sensitivity analysis of a multi-parameter ecological model was developed and used for the hydrodynamic-ecological model (DYRESM–CAEDYM, **DY**namic **RE**servoir **S**imulation **M**odel-**C**omputational **A**quatic **E**cosystem **D**ynamics **M**odel) applied to Lake Kinneret (Israel). Two different methods of sensitivity analysis, RPART (Recursive Partitioning And Regression Trees) and GLM (General Linear Model) were applied in order to screen a subset of significant parameters. All the parameters which were found significant by at least one of these methods were entered as input to a GBM (Generalized Boosted Modeling) analysis in order to provide a quantitative measure of the sensitivity of the model variables to these parameters. Although the GBM is a general and powerful machine learning algorithm, it has substantial computational costs in both storage requirements and CPU time. Employing the screening stage reduces this cost. The results of the analysis highlighted the role of particulate organic material in the lake ecosystem and its impact on the over all lake nutrient budget. The GBM analysis established, for example, that parameters such as particulate organic material diameter and density were particularly important to the model outcomes. The results were further explored by lumping together output variables that are associated with sub-components of the ecosystem. The variable lumping approach suggested that the phytoplankton group is most sensitive to parameters associated with the dominant phytoplankton group, dinoflagellates, and with nanoplankton (Chlorophyta), supporting the view of Lake Kinneret as a bottom–up system. The study demonstrates the effectiveness of such procedures for extracting useful information for model calibration and guiding further data collection.

1. Introduction

Computer models of ecosystems are increasingly used in order to predict possible impacts of policy measures prior to their implementation and to achieve a better understanding of these ecosystems (Ford, 1999). Success of ecosystem models is generally examined through comparisons to time-series of field data. However, when such comparisons are conducted, model predictions do not always match the observed data. The discrepancies can be attributed to various sources of error, such as estimation error of the initial conditions, sampling errors in the field data and errors in the model equations and parameters (Loehle, 1997). The considerable complexity of these models often requires the inclusion of a large number of parameters, many of whose values are uncertain.

Uncertainty in parameter values is attributed to the complexity of natural ecosystems and to the measures by which the parameters are obtained. Parameter values can be obtained from empirical observations or experiments, where the degree of uncertainty around the estimated value can be assessed and even reduced in most cases (Fieberg and Jenkins, 2005). If observations or experiments are not available, parameters can be derived from expert opinion or other models, yet such means are typically characterized by large uncertainty (Ray and Burgman, 2006). Moreover, models have various sensitivities to the different parameters. A parameter that the model is sensitive to is one that minor changes in its value would result in major changes in model output or inference. When high uncertainty in the value of a parameter coincides with high sensitivity of the model to that parameter, the reliability of model predictions may be very low (Bar Massada and Carmel, 2008).

In order to reduce the uncertainty associated with parameter values, considerable effort must typically be invested by the modeler. A prioritized list of influential parameters may be compiled. Such a list can be used to determine the parameters in

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doi:10.1016/j.envsoft.2010.06.010

which the reduction of uncertainty would result in the greatest increase in model accuracy and thus help prescribe resource allocation into further research (Thornton et al., 1979).

Sensitivity analysis (SA) may be used to qualitatively or quantitatively apportion the variation of the model outputs to different sources of variation in model components such as parameters, submodels and forcing data (Brugnach, 2005; Frey et al., 2004; Saltelli et al., 2000, 2008; Helton et al., 2006). Although SA is an optional element within the modeling process (Jorgensen, 1994), several modeling guidelines such as the EPA guidance document (2003) or the European Commission Impact assessment guidelines (2005) prescribe sensitivity analysis as a tool to ensure the modeling quality. SA is therefore considered an important stage in development of ecological models (Ravalico et al., 2005; Saltelli et al., 2000; de Young et al., 2004). In addition, SA can also have ecological importance by identifying the governing parameters and processes in a certain ecological system or even to improve model formulations (Thornton et al., 1979; Cariboni et al., 2007). For example, Cossarini and Solidoro (2008) found that the most relevant parameters in the trophdynamic model of the Gulf of Trieste (Northern Adriatic Sea, Italy) are those related to the growth formulation of the phytoplankton group, the decay rate of particulate organic phosphorus and the mortality rate of bacteria. Cariboni et al. (2007) applied a SA to a pelagic fish population model, revealing that the total order sensitivity index for larvae was ten times more than the total order of sensitivity index estimated for adult fish. These results indicate that from the fishing regulatory point of view the main effort has to be put into developing strategy for protecting young individuals.

Sensitivity analysis of model parameters is carried out by changing them and observing the corresponding response in the output variables. The change in the parameters is chosen on the basis of our knowledge of their acceptable ranges. In local SA, parameter values are changed one at a time, while fixing all other parameter values (Bar Massada and Carmel, 2008). Global SA is a group of techniques that alter a subset or all the parameters simultaneously in a given model simulation (Helton et al., 2006; Helton and Davis, 2003; Fieberg and Jenkins, 2005; Ginot et al., 2006; Chu et al., 2007; Marino et al., 2008). Global SA should probably be preferred in most situations, since (1) it accounts for the effects of interactions between different parameters, and (2) as ecological models are rarely linear, global SA does not assume a linear relationship between the parameters and state variables (Saltelli et al., 2000; Cariboni et al., 2007). Moreover, one may be interested in the relative impact of a group of parameters, a submodel or a process, which local SA is incapable of addressing.

A known shortcoming of global SA is the heavy computational demands (Hamby, 1994; Ascough et al., 2005; Moore and Ray, 1999). These become particularly limiting in models with tens or hundreds of parameters. Such complex models are ubiquitous in ecology, and it is not uncommon to find ecological models with 200 parameters or more. In such models, a single simulation run may last hours, even on powerful computers, and the number of simulations required for a significant global SA may be prohibitively large. SA of such models becomes an intricate and complex task which needs to be well thought out. Furthermore, sensitivity analysis outputs do not always provide the modeler with information on the effect of small changes (e.g. when the parameter is changed within its allowable domain) or how exactly several parameters interact with each other to effect a certain output variable.

Various criteria should therefore be considered when selecting an appropriate SA method (Ravalico et al., 2005; Ascough et al., 2005). The key criteria are: (1) the computational cost associated with an extensive SA (Hamby, 1994; Ascough et al., 2005; Moore and Ray, 1999), (2) the ability of the method to account for interactions between parameters, (3) the ability of the method to account for non-linearities and non-monotonicity often present in ecological models, (4) the input data required for the analysis, for example in many cases knowledge of parameter probability distributions is required but this knowledge is not always available, and (5) the ability to understand and use the output of the SA.

In this paper, a new global SA approach, applicable to multi-parameter models, was developed in order to satisfy the above-mentioned criteria. The approach combines several analysis methods. In the first step, two separate and independent analyses methods were performed: (1) based on general linear models (GLM) with random effects and with correction for multiple comparisons (i.e. a least squares method for fitting models that involves continuous and discrete variables); and (2) based on recursive partitioning and regression trees (RPART) which builds classification or regression models of a very general structure using a two stage procedure; the resulting models can be represented as binary trees. The outcomes of these two methods (i.e. the most sensitive parameters selected based on these two methods) were combined to generate a subset of parameters (for each output variable) to which the model was most sensitive. In the second step a more intricate quantitative method, a generalized boosted regression model (GBM, Friedman, 2001, 2002), was applied to the subset of parameters defined in the first stage. The GBM is a general, automated, data-adaptive modeling algorithm that can estimate the non-linear relationship between a variable of interest and a large number of covariates. The impact of the selected parameters on the output variables was estimated and the estimates were used to construct, for each one of the output variables, a final ordered list of parameters with a quantitative measure of the sensitivity of the output variables to the parameters.

The method was applied to a complex hydrodynamic-ecological model, **DY**namic **RE**servoir **S**imulation **M**odel-**C**omputational **A**quatic **E**cosystem **D**ynamics **M**odel, (DYRESM–CAEDYM and DYCD hereafter) used to study Lake Kinneret (Israel). In previously studies of DYCD performance, the seasonal variability and vertical variation in temperature, oxygen, and nutrients were successfully captured (Bruce et al., 2006; Gal et al., 2009), however, these studies also highlighted that much uncertainty exists in predicting nutrient–planktonic interactions that are highly non-linear and are less understood. Therefore the motivation of this analysis was centered on gaining deeper insights into these non-linear interactions. Although inference is not typically mentioned as a specific goal of sensitivity analyses, in this particular application the SA results were also used to derive insights into the model and into the properties of the actual ecosystem of Lake Kinneret.

2. Methods

2.1. DYRESM–CAEDYM (DYCD)

The 1-D hydrodynamic-ecological model, DYCD, developed at the Centre for Water Research, University of Western Australia (Hamilton, 1999; Imberger and Patterson, 1981) simulates the hydrodynamic and biogeochemical dynamics for aquatic ecosystems. DYRESM uses a Lagrangian approach for simulation of the hydrodynamics of aquatic ecosystems (Imberger and Patterson, 1981, 1989). Based on inflows, withdrawals, and meteorological conditions, it calculates the water level and changes to water temperature, salinity and stratification dynamics over time. The water column is represented by set of layers whose thickness ranges between 0.65 m and 2 m. DYRESM has been applied to lakes of varying types (Hamilton, 1999; Horn et al., 2001) including to Lake Kinneret (Gal et al., 2003).

CAEDYM dynamically couples with DYRESM to simulate nutrient cycling and various plankton groups and is the focus of the present SA analysis. CAEDYM consists of a series of partial differential equations to simulate time-varying concentrations of biogeochemical variables accounting for processes such as primary production, secondary production, nutrient cycling, oxygen dynamics and sediment-water interactions (Hipsey and Hamilton, 2008). Various configurations of the model have previously been validated in reservoirs, lakes (Romero et al., 2004;

Trolle et al., 2009; Bruce et al., 2006; Burger et al., 2007), estuaries (Robson and Hamilton, 2004) and the coastal ocean (Spillman et al., 2007, 2008) and were used, for example, to predict the impact of nutrient loading on various components in a lake ecosystem (Gal et al., 2009). A detailed description of the configuration, differential equations and parameterizations as applied to Lake Kinneret CAEDYM is given in Gal et al. (2009).

2.2. The study design

Out of a total of over 40 possible output variables, the current analysis focused on 20 key biological and chemical output variables during four different seasons (Table 1). Forcing time-series data (meteorology, inflows and outflows) from the year 1997 were used to drive the SA simulations. Model simulations were configured to run from January 1997 for a period of one year, with a 1-h time-step and daily output. Each output variable was calculated daily and averaged monthly over 12 months. To simplify the analysis, the 12 monthly values were divided into four groups representing the four seasons, so that the mean of each season was considered.

The SA was applied to 180 preselected parameters (Supplementary Table 3, the list of model parameters included in the SA, can be downloaded from http://envgis.technion.ac.il/Files/SA_Table_3.pdf). The parameters were selected based on their role in the dynamic equations of the key chemical and biological output variables and our experience with model calibration. Parameter values were assumed to be uniformly distributed over the defined ranges (see Supplementary Table 3 online). The simulated data for the SA, that is the sets of parameters used as input for the experimental simulations, were generated using Latin Hypercube Sampling (LHS, McKay et al., 1979; Helton and Davis, 2003). This is a popular choice for computer simulation experiments and for global sensitivity analysis (Santner et al., 2003; Helton and Davis, 2000, 2003). The LHS method was developed to help perform global uncertainty and sensitivity analyses involving computationally demanding models with large numbers of uncertain inputs and possibly large numbers of outputs and is geared for simultaneous study of any number of parameters (input factors). Specifically, let n be the number of experimental runs, and without loss of generality, assume that the possible values of each parameter belong to the unit interval [0,1]. The range of each parameter is divided into n non overlapping intervals of equal length on the basis of equal probability. One value is selected at random from each interval. The n values thus obtained for the first parameter are paired in a random manner (equally likely combinations) with the n values of the second parameter. These n pairs are combined in a random manner with the n values of the third parameter to form n triplets, and so on, until n 180-tuplets are formed. The number of experimental runs was taken to be $n = 1300$ as described below.

In this study only the results for the upper region (i.e. the 10 top meters of the water column) are analyzed. The output can be summarized by the vector $Y_i = (Y_{i1},\ldots Y_{i4})^T$ where Y_{ij} is the output of the ith output variable, $i = 1,\ldots,20$, at season j, $j = 1,\ldots,4$. Each one of the 20 output variables was analyzed separately.

The number of experimental runs was determined based on a General Linear Model (GLM) with mixed (random and fixed) effects; each consisting of 180 parameters (input factors). Each of the 20 GLMs included: (1) the season as a fixed effect; (2) 180 main fixed effects corresponding to the parameters; (3) 180×3 fixed interaction effects between each parameter and the season; (4) a random effect corresponding to the specific experimental run; and (5) a four-dimensional random effect vector corresponding to the specific season at each specific experimental run. The random terms of the model represent the departure of the model from the assumed linear model. This requires estimation of 724 ($4 \times 180 + 4$) regression coefficients and the variance matrix components that could include, at most, 10 distinct parameters. Our design was based on a total of 1300 experimental units, which is larger than the minimum required but is still feasible in terms of CPU time.

2.3. Sensitivity analysis

Below is a review of the statistical methods used in the analysis, emphasizing the advantages and disadvantages of each procedure.

2.3.1. The GLM with correction for multiple comparisons

GLM is a flexible generalization of least squared regression model. In the GLM with mixed effects, the observed output variables are considered to be influenced by two main sets of effects: fixed effects defining the expected values of the output variables, and random effects defining the variances and covariances of the output variables (Laird and Ware, 1982). Such models can accommodate correlated data within the subject and heterogeneous variances. We fitted 20 GLM models, one for each output variable, as described above in the Study Design. Specifically, each of the 20 models is defined as follows (Eq. (1))

$$Y_i = X_i\beta + Zd_i + \epsilon_i \quad i = 1,\ldots,1300 \tag{1}$$

where

$$X_i = \begin{bmatrix} 1 & 1 & 0 & 0 & x_{1i} & \ldots & x_{180i} & x_{1i} & \ldots & x_{180i} & 0 & \ldots & 0 & 0 & \ldots & 0 \\ 1 & 0 & 1 & 0 & x_{1i} & \ldots & x_{180i} & 0 & \ldots & 0 & x_{1i} & \ldots & x_{180i} & 0 & \ldots & 0 \\ 1 & 0 & 0 & 1 & x_{1i} & \ldots & x_{180i} & 0 & \ldots & 0 & 0 & \ldots & 0 & x_{1i} & \ldots & x_{180i} \\ 1 & 0 & 0 & 0 & x_{1i} & \ldots & x_{180i} & 0 & \ldots & 0 & 0 & \ldots & 0 & 0 & \ldots & 0 \end{bmatrix}$$

x_{ki} is the value of the k-th input factor ($k = 1,\ldots,180$) of simulation i after substracting the mean, $Z = (1,1,1,1)^T$; $\varepsilon_i = (\varepsilon_{1i}, \varepsilon_{2i}, \varepsilon_{3i}, \varepsilon_{4i})^T$ is a random vector assumed to be independently distributed with zero mean; β is a 724-dimenstional vector of unknown parameters corresponding to the columns of X_i, and d_i is a random effect with a mean of zero. The distributions of ϵ_i and d_i are assumed to be independent. It should be noted that $Zd_i + \epsilon_i$ represents the departure from the linear model $X_i\beta$.

The analysis was performed using a restricted maximum likelihood method with an unrestricted covariance matrix, namely, no specific structure is assumed in estimating the covariance matrix for estimating $\mathrm{Var}(Y_i) = Z\mathrm{Var}(d_i)Z^T + \mathrm{Var}(\epsilon_i)$ since it fitted our data better than the other more specific covariance matrix structures. The main advantages of this method are: (1) it provides a p-value for each effect included in the model, which can be used to decide which parameters significantly contribute to the model; (2) the interaction terms between season and each of the 180 input variables are easily included and the results can be interpreted; (3) the results of each model can be easily corrected for multiple comparisons by using the well-known false discovery rate (FDR) method (Benjamini and Hochberg, 1995).

The GLM along with the FDR analyses were performed using the SAS software. The final list of the p-values can serve as a basis for selecting the best subset of parameters. The main limitation of this model is the linearity assumption. This assumption is not made in the following RPART analysis.

Table 1
A list of model output variables considered in the SA. Each variable includes 4 notations representing the four seasons where the suffixes 1q, 2q, 3q and 4q represent winter, spring, summer, and autumn, respectively. For example, DINOF 1q stands for Dinoflagellates in winter, DINOF 2q stands for Dinoflagellates in spring, etc.

Output variable	Variable name	Units	Notation
y_1–y_4	DINOF: Dinoflagellates	mgC L^{-1}	DINOF 1q–4q
y_5–y_8	CYANO: *microcystis*	mgC L^{-1}	CYANO 1q–4q
y_9–y_{12}	DO: Dissolved oxygen	mgO L^{-1}	DO 1q–4q
y_{13}–y_{16}	ZOOP2: Herbivorous zooplankton	mgC L^{-1}	ZOOP2 1q–4q
y_{17}–y_{20}	ZOOP3: Micro zooplankton	mgC L^{-1}	ZOOP3 1q–4q
y_{21}–y_{24}	ZOOP1: Predatory zooplankton	mgC L^{-1}	ZOOP1 1q–4q
y_{25}–y_{28}	NOUDUL: *Aphanizomenon ovalisporum*	mgC L^{-1}	NOUDUL 1q–4q
y_{29}–y_{32}	FDIAT: *A. granulate* (diatoms)	mgC L^{-1}	FDIAT 1q–4q
y_{33}–y_{36}	Chlorophyta: Nanoplankton	mgC L^{-1}	CHLOR 1q–4q
y_{37}–y_{40}	PO_4: Inorganic phosphorus	mgP L^{-1}	PO4 1q–4q
y_{41}–y_{44}	NO_3: Nitrate	mgN L^{-1}	NO3 1q–4q
y_{45}–y_{48}	NH_4: Ammonium	mgN L^{-1}	NH4 1q–4q
y_{49}–y_{52}	DIC: Dissolved inorganic carbon	mgC L^{-1}	DIC 1q–4q
y_{53}–y_{56}	DOCL: labile dissolved organic carbon	mgC L^{-1}	DOCL 1q–4q
y_{57}–y_{60}	POCL: labile particulate organic carbon	mgC L^{-1}	POCL 1q–4q
y_{61}–y_{64}	POPL: labile particulate organic phosphorus	mgP L^{-1}	POPL 1q–4q
y_{65}–y_{68}	DOPL: labile dissolved organic phosphorus	mgP L^{-1}	DOPL 1q–4q
y_{69}–y_{72}	PONL: labile particulate organic nitrogen	mgN L^{-1}	PONL 1q–4q
y_{73}–y_{76}	DONL: labile dissolved organic nitrogen	mgN L^{-1}	DONL 1q–4q
y_{77}–y_{80}	NITRF: Nitrification rate	mgN L^{-1}	NITRF 1q–4q

2.3.2. Recursive partitioning and regression tree (RPART)

The RPART procedure grows a hierarchical tree that is useful for capturing complicated non-linear relationships, in addition to the interactions among the parameters, as is almost always the case in complex simulation models. RPART implements the ideas of Classification and Regression Trees (Breiman et al., 1984): a tree-based modeling exploratory technique that is particularly useful for screening variables and summarizing large multivariate datasets. RPART is an iterative process of splitting the data into partitions, and then splitting it up further on each of the branches. Initially, all of the records are together in one box. The algorithm then disaggregates the data using every possible binary split on every field. The algorithm chooses the split that partitions the data into two parts such as to minimize the sum of the squared deviations from the mean in the separate parts. This splitting or partitioning is then applied to each of the new branches. The process continues until each node reaches a user-specified minimum node size and becomes a terminal node. If the sum of squared deviations from the mean of all simulations in a node is zero, then that node is considered a terminal node even if it has not reached the minimum size. The predicted value of the output variable for a particular node is the sample average of the output variable consisting of records included in that node.

The parameters selected to be included in the final tree can be considered as the subset of parameters that are important for the model. However, in contrast to the GLM analysis of Section 2.3.1, it is not clear how to rank the parameters according to their contribution, since two different trees can perform equally well. After building a complete tree, possibly large or complex, we must decide how much of that model to retain. This stage of pruning the tree is done by a cross-validation method. For a comprehensive description of the RPART analysis the reader is referred to Therneau and Atkinson (1997) and references therein. An example for the use of RPART method in sensitivity analysis of ecological modeling is given in Deygout et al. (2009).

The RPART analysis was performed for each of the 20 output variables separately and included all 180 parameters and the season effect. For each model, a 20-fold cross validation analysis was performed. The analysis was performed by using the RPART routines of R and is available at http://cran.r-project.org/web/packages/rpart/index.html.

In the light of the advantages and disadvantages of the GLM and RPART techniques, we believe that a more reliable picture can be provided by uniting the results of these two models. That is, based on these two methods we constructed a subset of parameters consisting of all the parameters included in at least one of the two techniques. From the GLMs we collected all the parameters that were significant after the FDR correction for multiple comparisons, at a significance level of 0.05. From the RPART analysis we included all the parameters used in the tree. This resulted in 20 subsets of parameters one for each output variable. Each subset was then used in the analysis of generalized boosting regression models, as described below.

2.3.3. Generalized boosted regression model (GBM)

The "boosting" procedure is a way of combining the performances of many "weak" classifiers to produce a powerful one. In boosting regression methods (Friedman, 2001; 2002) a sequence of very simple trees are computed, where each successive tree is built for residual prediction of the preceding tree. It can be shown that such trees can eventually produce an excellent fit of the predictive values to the observed values, even if the specific nature of the relationship between the outcome variable and the predictor variables is non-linear in nature. Hence this method represents a general and powerful machine learning algorithm. Specifically, given a "training sample" our goal is to find a function $F^*(x)$ that maps the input vector x to Y and minimizes the expected value of some pre-specified loss function. Boosting approximates $F^*(x)$ by an additive expansion of the form

$$F(x) = \sum_{m=0}^{M} \alpha_m h(x; a_m) \tag{2}$$

where the functions $h(x;a)$ are usually chosen to be simple functions of x with parameters $a = (a_1, a_2, \ldots)$. The reader is referred to Friedman (2002) for the possible algorithms for finding such $F(x)$. GBM analysis also provides the relative importance or relative influence of each parameter. This measure is based on the empirical improvement in the loss function (e.g. squared error loss) due to the split on the specific parameter in a tree, averaged over all the trees generated by the boosting algorithm. This score of relative influence serves as the key measure for our final conclusion of the analysis, as elaborated below.

However, this flexible GBM analysis, in contrast to the GLM and RPART analyses, has substantial computational costs, in both storage and CPU time. Hence, we included in this analysis only the parameters already identified by the GLM or the RPART analyses as being the most important.

The GBM method of Friedman (2001) was separately applied to each of the 20 output variables, using the GBM package of R available at http://cran.r-project.org/web/packages/gbm/index.html. Each GBM analysis was based on the mean squared loss function; ANOVA model with three–way interactions; 10000 trees; 5-fold cross validation; and half of the data used for training. Each list constructed in the GBM analysis consisted of the selected parameters ordered according to their relative influence on the particular output variable. The relative influence is a score between 0 (no influence) to 100 (complete influence) and the sum of scores over all selected parameters in each model equals 100.

2.3.4. Final scoring and ranking procedures

In order to combine the results of the 20 GBMs and provide a final list of the most influencing parameters, we listed the ten most important parameters of each output variable. These were then merged into groups according to their functionality in the model. For example x_1–x_5 form a group since they relate to "Maximum potential growth rate of phytoplankton". In total we had 47 functional groups.

Let Z_{jm} be the relative influence of the m-th parameter that belongs to the j-th functionality group, $m = 1,\ldots,M_j$ $j = 1,\ldots,47$ where M_j is the number of selected parameters in the functionality group j. Then, we define the sum and the mean influence score of the functional group j by:

$$\mathrm{SIS_j} = \sum_{m=1}^{M_j} Z_{jm} \tag{3}$$

and

$$\mathrm{MIS_j} = \frac{1}{M_j} \sum_{m=1}^{M_j} Z_{jm} \tag{4}$$

respectively.

Ranking procedure: In addition, instead of using the actual value of the relative influence Z_{jm}, we ranked the 10 most important parameters of each output variable from 1 (low influence) to 10 (high influence). If a parameter is not included in the top 10 parameters, in a specific model out of the 20 models, its rank is set to be 0 in the specific model. Let R_{ij} be the rank of parameter i in model j $i = 1,\ldots,180$, $j = 1,\ldots,20$. Thus, the total rank of each parameter is defined as

$$TR_i = \sum_{j=1}^{20} R_{ij} \tag{5}$$

After following the ranking procedure, 77 parameters (out of 180) had rank greater than zero. We prefer using the sum of score rankings rather than the sum of score values since the latter may be highly influenced by extreme score values. The ranking procedure was also employed for ranking groups of variables, for example the variables associated with phytoplankton or zooplankton.

3. Results

The analysis consisted of 1288 simulations (12 simulations were excluded due to technical problems). The most notable difference between the results obtained using the RPART and GLM analyses was the higher number of parameters identified as important by the RPART method. For example, y_1–y_4 (the output variable dinoflagellates) had 27 parameters selected by RPART and 14 parameters selected the GLM (including the season affect). Most of the parameters that were selected by the GLM procedure were also identified by the RPART (Supplementary Table 4, the results of the GLM and RPART methods, can be downloaded from http://envgis.technion.ac.il/Files/SA_Table_4.pdf). One of the advantages of the GLM procedure is that it allows exploring the sensitivity to the parameter in the different seasons. For example, the output variables: y_1, y_2, y_3, and y_4 are related to the results of the sensitivity analysis of dinoflagellates in winter, spring summer and autumn, respectively. The results indicate that dinoflagellates are sensitive to some parameters throughout the whole year, such as the parameter "Minimum internal N ratio for *Peridinium*" (x_{31}), and sensitive to other parameters only during certain seasons. For example, the parameter "Nutrient dependent migration velocity for *Peridinium*" (x_{90}) was selected by the GLM only in the autumn (data not shown).

The GBM model was fitted using as input all the parameters selected by RPART and the GLM procedures. The quantitative measures of the GBM analysis for the highest ranked ten parameters for each one of the 20 output variables are shown in Fig. 1. Parameters referring to the same attribute were merged under the same name (see Section 2.3.4 for explanations) and therefore some output variables have less then 10 parameters. We employed three different approaches to explore the results. In the first approach the model was considered as a whole (i.e. all the output variables were considered). Unsurprisingly, seasonality was found as an important factor for all biological and chemical components. The mean GBM score of the sensitivity was 20 (out of

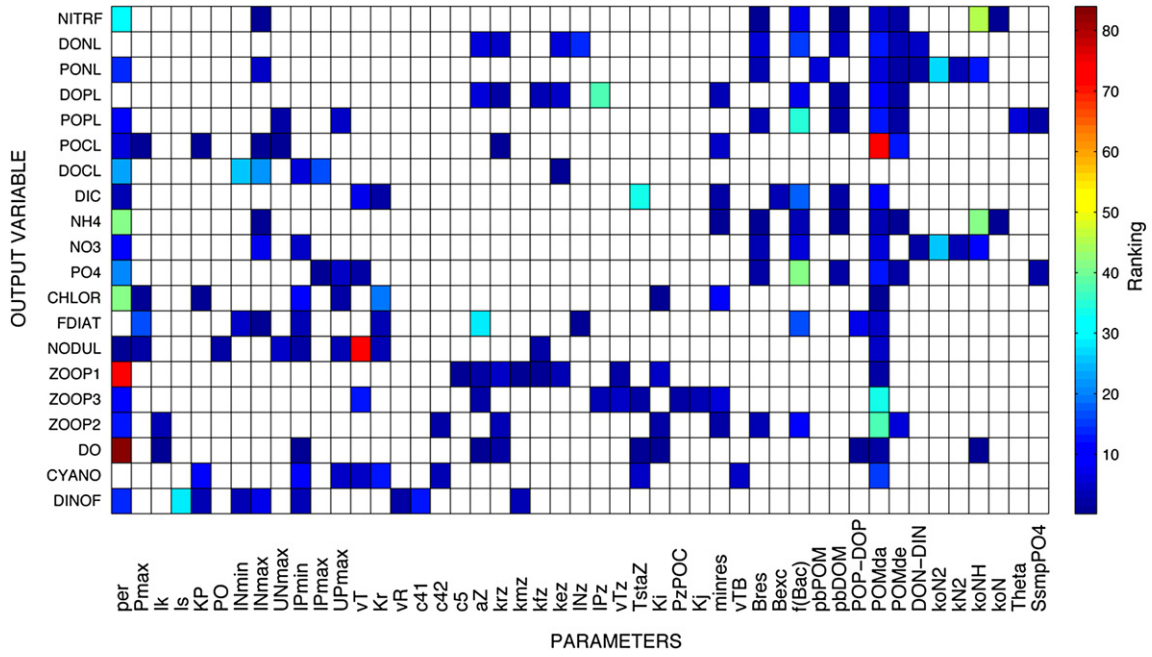

Fig. 1. Quantitative measures of the GBM analysis. For clarity, only the highest ranked ten parameters for each one of the 20 output variables are shown. Red represents high score values (maximum possible score value is 100) and blue indicates low score values. The term "Per" stands for the season. Parameters referring to the same attribute were presented in the figure under the same name, for example, the parameter name "P_{max}" stands for x_1–x_5 which are the parameters Maximum potential growth of the five phytoplankton groups represented by *Peridinium*, *Microcystis*, *Aphanizomenon ovalisporum*, Chlorophyta and *Aulacoseira granulate,* respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

maximum score of 100). In 80% of the output variables, seasonality was ranked as one of the 10 most influential parameters. Seasonality however is not a parameter in the model or the focus of the analysis and therefore was not included in the remaining analysis. Most of the output variables were also sensitive to two additional parameters: particulate organic material (hereafter, POM) diameter (POMda, x_{167}) and POM density (POMde, x_{168}). The sum of influence scores (i.e. the sum of the GBM scores) and the mean influence score are means to measure influence (Table 2). A parameter may have a high total sum of influence scores with a low mean influence score which means that a large number of output variables were sensitive to that parameter at a relatively low significance (for example, the parameter "Maximum internal N to C ratio for Phytoplankton", x_{36}–x_{40}). It is also possible that a parameter will have a low sum of influence scores with a high mean influence score value which means that a small number of output variables are very sensitive to that parameter (for example the parameters "Denitrification rate coefficient", x_{173}). As with the scoring results, the results of the ranking procedure (Fig. 2) indicate the importance of the particulate organic material. However the ranking procedure also demonstrates the influence of other parameters such as parameters associated with bacteria, for example the "Half saturation constant for bacteria" or the "Respiration rate of bacteria".

The second approach was to examine the sensitivity of a specific output variable as opposed to using all the output variables as in the previous approach. For example, the GBM scores of the ten most significant parameters affecting the output variable nanoplankton (Chlorophyta) were explored (Fig. 3A). Nanoplankton was found to be sensitive to parameters such as "Respiration rate coefficient" (x_{81}) and "Minimum internal N ratio" (x_{34}). A similar analysis for the predatory zooplankton indicated that 80% of the parameters to which this output variable is sensitive were directly related to the zooplankton sub-model. The other parameters were related to one of its prey types and to POM diameter (Fig. 3B). Similarly, the output variable NO_3 (Fig. 3C) was sensitive mainly to parameters associated with the nitrogen cycle, such as "Nitrification rate coefficient" (x_{176}), "Denitrification rate coefficient" (x_{173})

Table 2
Integrated GBM results: sum of the influence scores (Eq. 3), number of occurrences and mean influence score (Eq. 4)of the 10 most influencing parameters. Parameters are ordered by decreasing sum of scores values. Parameters referring to the same attribute were merged (for example the parameter "Temperature multiplier for phytoplankton growth" represents parameters x_{63}–x_{67} which are the temperature multiplier of the five phytoplankton groups).

Parameter (name and number)	Sum of influence score	Number of occurrences	Mean influence score
Particulate organic material diameter (x_{167})	250.5	18	13.92
Half saturation for bacteria (x_{161})	159	10	15.9
Nitrification rate coefficient (x_{176})	108.4	5	21.68
Temperature multiplier for phytoplankton growth (x_{63}–x_{67})	97	6	16.17
Denitrification rate coefficient (x_{173})	53	2	26.5
Messy feeding rate of Zooplankton (x_{93}–x_{95})	43.9	6	7.32
Maximum internal N to C ratio for Phytoplankton (x_{36}–x_{40})	43.88	11	3.99
Zooplankton internal phosphorus (x_{111}–x_{113})	41.5	2	20.75
Phytoplankton respiration coefficient (x_{78}–x_{82})	40.8	5	8.16
Minimum internal P to C ratio for Phytoplankton (x_{46}–x_{50})	40.68	10	4.07

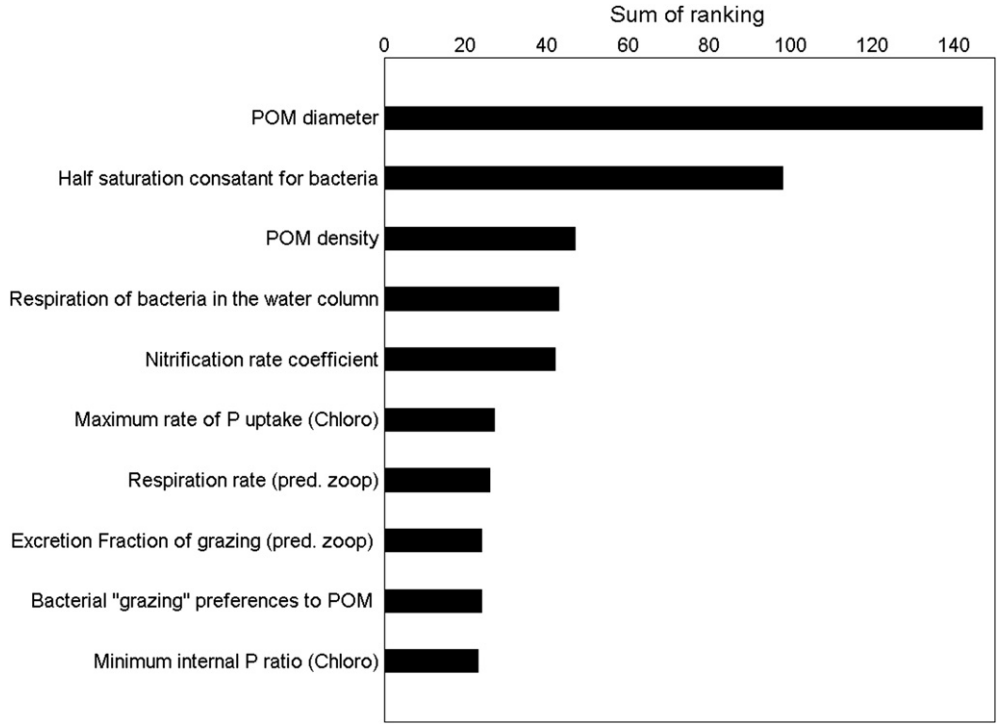

Fig. 2. Sum of parameter ranks across all output variables.

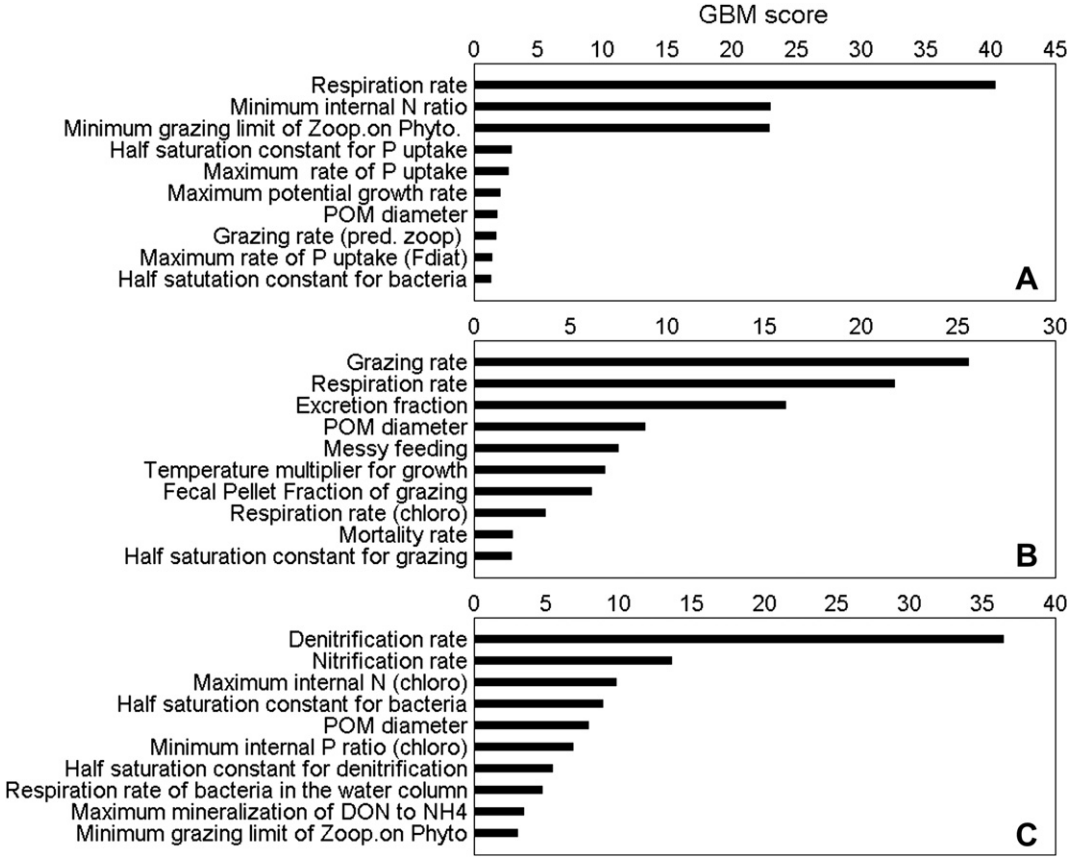

Fig. 3. The GBM score (out of 100) of the highest ranked parameters for the output variable: (A) nanoplankton (Chlorophyta), (B) predatory copepod, and (C) NO_3.

and "Maximum mineralization of DONL to NH4" (x_{171}). However NO_3 was also sensitive to indirect parameters such as the "Minimum internal N ratio" and "Minimum internal P ratio" of Chlorophyta" (x_{34} and x_{49}, respectively). These three output variables: nanoplankton, predatory copepods, and NO_3, although related to different biological and chemical groups, were all very sensitive to POM diameter (x_{167}).

The third approach used to explore the results was to lump together output variables associated with a specific ecosystem component of interest and rank the integrated GBM results linked with that group of variables. For example, lumping together all the phytoplankton output variables into a single group verified that, except for POM diameter, the parameters to which this group was most sensitive were associated with dinoflagellates and nanoplankton (e.g. respiration rate coefficient, nutrient uptake, light saturation for maximum production and internal P to C ratio, Fig. 4A). Focusing on nitrogen related output variables such as NO_3, NH_4, PONL (labile particulate organic nitrogen), DONL (labile dissolved organic nitrogen) and nitrification rate, reveals that they were sensitive mainly to bacteria and POM parameters and to parameters related to processes such as nitrification, denitrification and mineralization (Fig. 4B).

The GBM results also provided a means to examine in more detail the relationship between the output variable and the parameters to which it was sensitive. Namely, it is possible to determine whether the variable is sensitive to the parameters over the entire range of parameter values or to a more limited range. For example, Fig. 5A is a marginal plots demonstrating the sensitivity of the output variable dinoflagellates to the parameter "Light saturation for maximum production" (x_{10}) over the entire range of x_{10} (measured on a relative scale of 0–100). Dinoflagellates are sensitive to x_{10} at relatively high parameter values (e.g. at scaled values higher than 80). It is also sensitive to the parameter "Light dependent migration velocity of dinoflagellates" (x_{88}) more uniformly across the parameter range (e.g. at scaled values higher than 30). However, the magnitude of the sensitivity is higher to x_{10} than to x_{88} when x_{10} is at the upper portion of its range. The higher degree of sensitivity to x_{10} at higher values demonstrates a value-specific sensitivity to that parameter which is important for calibration purposes.

The GBM results further allow exploring the interaction and combined effects of two (or three) parameters. The interaction can be examined through the use of two-way plots. The two parameters described above, x_{10} and x_{88}, are used as an example. The result (Fig. 5B) indicates that the greatest impact (where the plot color is cyan) is when the value of both parameters, x_{10} and x_{88}, is relatively high (e.g. >80). Through the use of these types of plots it is possible to study the joint influence on the output variable dinoflagellates. It is also possible to examine the same interaction separating between the four seasons (Fig. 5C). It is evident from the example that the interactions between the parameters and the impact on the output variable are season-dependent with a larger effect occurring during periods 2–4 (spring to autumn).

4. Discussion

In this study we implemented a new approach to conducting a global sensitivity analysis for multi-parameter complex ecological models. The computational cost associated with the method is largely reduced since the analysis employs a "screening" stage using a relatively fast method to identify a subset of sensitive parameters that is subsequently used as input to the more intricate

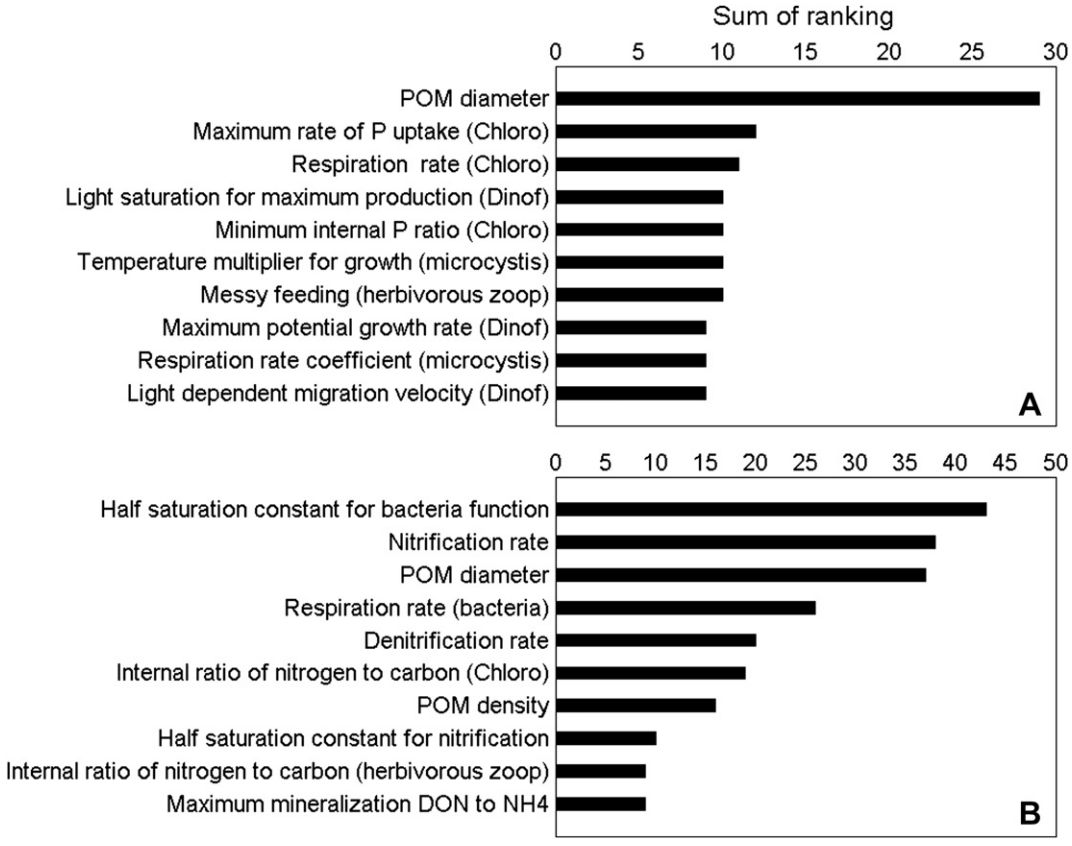

Fig. 4. Sum of parameter ranks for (A) the phytoplankton component, and (B), Nitrogen related output variables.

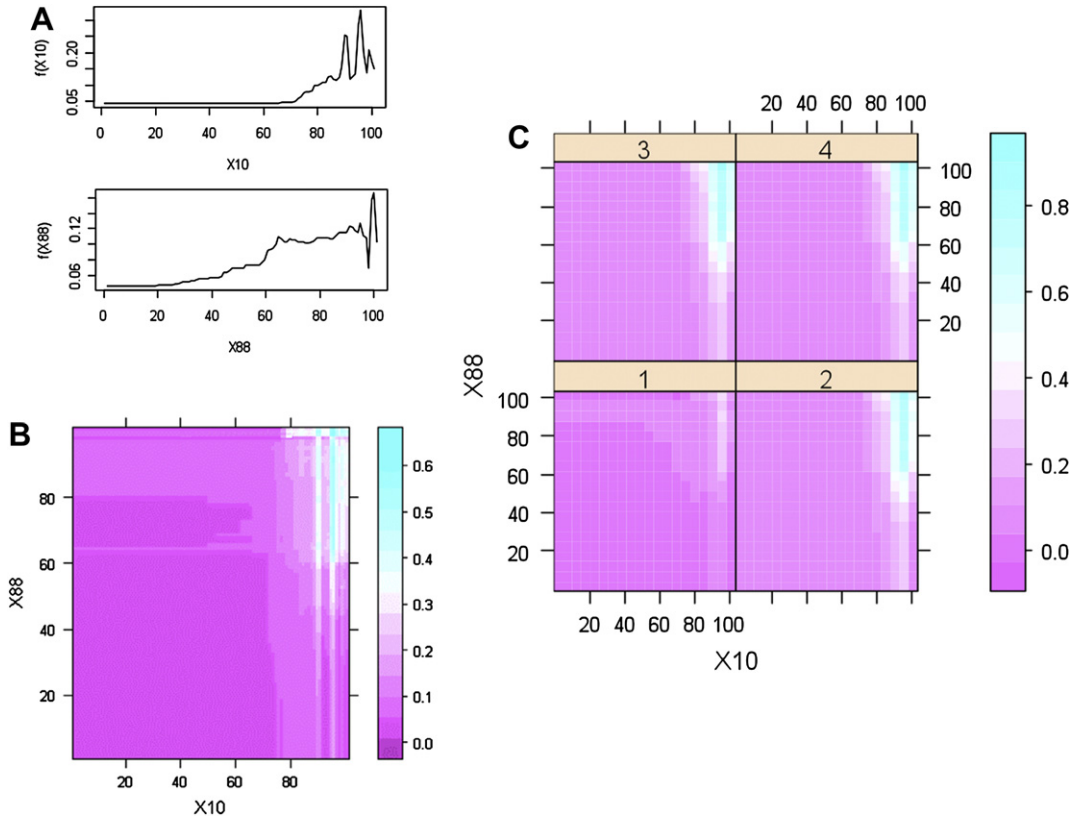

Fig. 5. An example of the visual and detailed analysis of the GBM results. In this example we show the impact of two parameters, x_{10} ("Light saturation for maximum production") and x_{88} ("Light dependent migration velocity") on the output variable Dinoflagellates. The parameters were scaled to the interval [0–100] where 0 is the lowest boundary and 100 is the highest boundary of the interval and the effect was measured using a relative scale, 0–1. (A) Marginal plots of the parameters showing the effect of small changes in their values, within the allowable domain, on the output variable. (B) A two-way plot of the combined effect of the two parameters on the output variable, Pink indicates low effect and the cyan indicates higher effects, and, (C) Three-way plots of the combined effect of x_{10} and x_{88} on the output variable in winter (1) spring (2), summer (3), and autumn (4). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

and computationally intensive GBM method (criterion one of Ravalico et al., 2005). The GBM method accounts for linear and non-linear interactions that are common in complex ecological models. Except for the need to define the allowable domain for each parameter, the procedure for generating the simulated data (LHS) assumes uniform probability distribution to all parameters and therefore does not require any knowledge of the probability distribution of the parameters as required in other commonly used methods (Sobol, 1993; Morris, 1991). The outcome of the GBM provides a quantitative measure of the sensitivity of the output variables to the different parameters, as well as complementary information such as the impact of small changes of a specific parameter on a specific output variable, and how several parameters interact with each other to manifest in changes to an output variable.

Various techniques have been proposed to address SA. The Morris method (Morris, 1991) produces sensitivity estimates to the total effect due to a *single* parameter. Several simple *linear* regression analysis and correlation measures are also commonly used, such as the Pearson correlation coefficient, the partial correlation coefficient and standardized regression coefficient. For non-linear but monotonic relationship, rank-based measures can be used, such as Spearman rank correlation coefficient. Fourier Amplitude Sensitivity Analysis (FAST) (Cukier et al., 1978), Extended FAST (Saltelli et al., 1999) and Sobol' method (Sobol, 1993) deal with non-linear and non-monotonic trends and provide measures of the main effect of each parameter or group of parameters and higher order effects. However, these methods cannot be applied with high number of parameters, such as 180 in our case (Caraboni et al., 2007).

Storlie and Helton (2008a) and Storlie and Helton (2008b) compared between various multiple predictor smoothing methods based on non-parametric regression techniques and concluded that non-parametric regression procedures can yield more informative SA compared to traditional parametric regression models, given that the relationships between model inputs and model outputs are non-linear. Storlie et al. (2009) provided an overview of several modern non-parametric techniques. They also compared between the models by simulation study consists of 2–10 parameters. In models like ours, non-parametric regression cannot be applied due to the large number of parameters and output variables.

Our method satisfies all the desired criteria of Ravalico et al. (2005): it can handle 180 parameters; regression trees consider interactions, non-linear effects and non-monotone effects; and the output provides a direct measure of the relative importance of each parameter.

Our approach was tested on the complex hydro-ecological model DYCD, as applied to Lake Kinneret. The sensitivity analysis for twenty output variables over four seasons was applied to 180 parameters in 1300 simulations. The outputs of the two analyses methods were similar; however the RPART yielded more significant parameters than the GLM analysis (see Supplementary Table 4 online). Each sensitivity analysis method is typically based on different assumptions regarding appropriate ways of measuring sensitivity, and it is expected that they lead to different results. The

GLM also provides means to examine differences in sensitivity among the four seasons. The advantage of employing two different analysis methods is that it ensures consideration of a larger number of parameters and thereby lowers the chance of overlooking parameters because of shortcomings of a particular method.

Different approaches can be adopted in order to explore and use the quantitative measures provided by the GBM outcome. Selecting a certain approach is dependent on the purpose of the calibration (i.e. adjusting model parameters so that outputs best match observed data) and the aim of the model. If the modeler is interested in a specific output (such as "nanoplankton" for example) then the calibration effort should be concentrated on the parameters to which the specific output is sensitive (Fig. 3). If the modeler's interest is in the operation of the model as a whole, then the integrated output of the GBM results should be considered as the target for the calibration effort (Fig. 2). Calibration aimed to improve model results for a large number of output variables (or processes) will concentrate on parameters with high mean ranking values given that they have a large number of occurrences, for example the parameter "POM diameter" which has 18 out of 20 possible occurrences would be a good target in that case (Table 2). Grouping the GBM results of several output variables that are related to each other, for example, grouping all the output variables related to zooplankton or phytoplankton, allows the modeler to improve the calibration for a subset of output variables.

Studying the ecological implications of the SA output can enhance our understanding of key ecosystem dynamics. Basic factors driving the ecosystem such as sunlight, wind, mixing and sediment oxygen demand are necessary to capture factors such as lake temperature (stratification and de-stratification), dissolved oxygen and light (photic zone) dynamics. In particular, many processes, and the associated model state variables in Lake Kinneret are largely shaped by seasonal drivers (Serruya, 1978; Pollingher, 1981, 1986; Berman et al., 1995; Zohary, 2004; Gophen, 2005). These factors have been accurately modeled by previous studies using DYCD (Gal et al., 2009; Bruce et al., 2006) and provide the necessary environmental settings on which the nutrient and plankton dynamics are based. Thus, their related parameters were excluded from the SA and the analysis was focused particularly on gaining insights to key parameters associated with the non-linear interactions between nutrients and planktonic components in the surface layer. Accordingly, the results reflected the important role that seasonality plays, as indicated by the factor "per", which was found to be the most significant for most output variables. While there may be some interaction between the nutrients and planktonic components and the temperature structure or oxygen concentrations, these feedbacks were considered minor for the purposes of demonstrating the new SA method.

The most important parameter, after seasonality, was the "POM diameter" (Fig. 2). The high ranking for this parameter can be explained by the fact that the POM diameter is a key parameter in processes related to sedimentation of particulate nutrients, which is a core mechanism used to balance the nutrient budget in the lake. The parameters "POM diameter" and "POM density" are often used as tuning parameters for controlling these elementary processes. Ecologically, this means that a dominant system driver is the balance of nutrients in the lake, which is highly regulated by sedimentation processes. Surprisingly, the number of publications related to POM composition (Stiller, 1977; Grossart et al., 1998; Hadas et al., 2009) and particularly to POM sedimentation (Zohary et al., 1998; Yacobi and Ostrovsky, 2008; Viner-Mozzini et al., 2003; Gal et al., 2009) are fewer than expected considering the importance of these process as indicated in this analysis. This highlights the need to prioritize further study of sedimentation and recycling rates of particulate detrital material, and exemplifies the potential role of SA in identifying key factors and processes in the model as well as in actual systems.

The importance of nutrient-related process was also confirmed by the high ranking of parameters such as "Half saturation constant for bacteria" (x_{161}) and "Respiration rate of bacteria" (x_{159}) that are related to bacterial mineralization processes of organic material which is also a key process for regulating nutrient recycling rates. This is in accordance with recent publications, suggesting the bacteria are a major biological agent for organic carbon cycling in Lake Kinneret (Berman et al., 2004; Hart et al., 2000). Thus, apart from seasonality, the most significant parameters for the ecosystem are related to nutrients and the governing processes of sedimentation and transformation of material between the particulate, dissolve, organic and inorganic forms. Next in importance are parameters related to the primary and secondary producers in the ecosystem (mainly nanoplankton and predatory zooplankton). According to the SA, these results indicate that the ecosystem can be described as bottom-up controlled system (but see Gophen, 2003 for an opposing view).

The GBM results confirm that most of the output variables were sensitive mainly to parameters associated with the specific output i.e. parameters that are part of the equations used to calculate the output variable in question. Hence these results serve as an empirical validation of the methods. For example, the output variable NH_4 was most sensitive to the parameter "nitrification rate coefficient". Similarly, the output variable dinoflagellate was found to be highly sensitive to the parameter "Light saturation value at which production is maximal" (x_{10}) and "Light dependent migration velocity" (x_{88}). This is consistent with the literature describing the dependence of phytoplankton on light and specifically the aggregation dynamics of the Lake Kinneret dinoflagellate *Peridinium* around the depth of optimal light intensity. Dinoflagellates are characterized by daily vertical migration, including active movement towards the layer with optimum light intensity (during the light hours) or temperature (Prezelin and Sweeney, 1979; Dubinsky and Berman, 1981; Sukenik, 2008).

However, some output variables were sensitive to parameters that were not directly related to them, thereby demonstrating the usefulness of the method for exploring the ecosytem. For example, the state variable DOPL (labile dissolved organic phosphorous) was very sensitive to the parameter "internal phosphorus ratio of zooplankton" (IPZ, Fig. 1). This is in line with Bruce et al. (2006) who pointed out that excretion of dissolved nutrients by zooplankton, accounts for 3–46% and 5–58% of phytoplankton uptake of phosphorus and nitrogen, respectively. Additionally, Hambright et al. (2007) showed that microzooplankton grazing and nutrient mineralization are driving forces affecting bacteria and phytoplankton dynamics, playing important roles in carbon and nutrient transfer to upper trophic levels. Our results therefore suggest that future effort should be focused on the interactions between internal N and P of zooplankton and mineralization of the organic matter in Lake Kinneret.

Interestingly, exploring SA results in the context of the different biological groups (e.g. phytoplankton group or zooplankton group) revealed that while some parameters are common to most of the output variables in the group, some output variables are sensitive to exclusive parameters. For example, most of the phytoplankton output variables are sensitive to the "Minimum internal P ratio" and the "Respiration rate coefficient" although *Aphanizomenon ovalisporum* (output variable: NODUL), for example, is particularly sensitive to "Temperature multiplier for growth". Some studies have linked Lake Kinneret water temperature and *A.ovalisporum* blooms, suggesting an actual pathway for the importance of temperature related parameters and their effect on *A.ovalisporum* biomass. Pollingher et al. (1998) reported unusually high water

temperatures and low wind inputs observed in the lake prior to, and during, the first appearance of *A.ovalisporum* bloom period in Lake Kinneret in 1994, and the onset of stormy conditions, fall in water temperatures and phosphorus limitation as the lead to the demise of the bloom (Hambright et al., 2001).

The GBM results can provide information on the sensitivity of each output variable to each parameter as it changes within its acceptable domain. This information can be used to reduce calibration effort. Studying two-way and three-way interactions provides even deeper insight into linear and non-linear interactions between different parameters and has implications for future research. For example, exploring the mutual impact of two parameters such as "light saturation for maximum production" and "Light dependent migration velocity" on dinoflagellates demonstrate that both values have to be high enough in order to have an influence on the dinoflagellate output variable (Fig. 5).

While the outcome of the SA can be useful for improving model calibration, the possibility of achieving different results if the simulation period was longer should be considered. The reason for that is the time lag required for some of the output variables to stabilize as some models even require an acceleration (spin-up) period to stabilize the model, or the possible difference between the short- and long-term results. We did not explore this issue, and further analysis is required to explore the possible impact of long-term simulations on the results of SA.

The new sensitivity analysis method implemented in this study has allowed us to single out and rank the parameters to which the model is most sensitive, thereby providing a method to prioritize our research efforts in order to improve parameter estimation for the model. Furthermore, the sensitivity analysis results provided a unique option to deepen and extend our understanding of the importance of functional interrelations within the ecosystem.

Acknowledgments

This research was supported by grants from the Ministry of Science and Technology Israel, the Federal Ministry of Education and Research, Germany (BMBF) and the Israel Water Authority. Support for V.M. was provided by the Yohay Ben-Nun Scholarship fund and The Australia-Israel Scientific Exchange Foundation. We thank the anonymous reviewers for their constructive comments and suggestions.

Appendix. Supplementary material

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.envsoft.2010.06.010.

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