



A commentary on the modelling of the causal linkages among nutrient loading, harmful algal blooms, and hypoxia patterns in Lake Erie



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ABSTRACT

In this study, our primary aim is to evaluate the capacity of past and current modelling efforts to depict the causal relationships between major water quality indicators (e.g., chlorophyll *a*, harmful algal blooms, dissolved oxygen) and nutrient loading in Lake Erie. We first conduct a review of nearly all the modelling projects documented in the pertinent literature, and then evaluate the performance of six of these models applied over the past thirty years. We examine the strengths and weaknesses of the different modelling strategies, their adequacy in representing the processes underlying plankton dynamics, and their ability to reproduce the spatiotemporal variability in hypoxia or harmful algal blooms. Our analysis shows that these models have mainly offered heuristic tools to examine different ecological hypotheses and dictate future data collection efforts. Our study critically discusses the most appropriate next steps to improve the reproduction of the spatiotemporal patterns of major phytoplankton groups, e.g., cyanobacteria, the functional role of dreissenid mussels, and the relative importance of diagenesis processes on the manifestation of hypoxia in Lake Erie. Finally, we advocate the standpoint that a single “correct” strategy does not exist, and therefore we should strive for a synthesis of multiple modelling approaches which can contribute to an integrative view on the functioning of the system.

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Introduction

Environmental modelling has been an indispensable tool for addressing lake eutrophication. A variety of *data-oriented* and *process-based* models have been used to examine the impact of nutrient loads to ecosystem integrity and to set water quality goals. The data-oriented (or empirical) models are mainly steady-state, mass-balance approaches that predict lake total phosphorus (TP) concentrations as a function of lake morphometric/hydraulic characteristics, such as the areal phosphorus loading rate, mean depth, fractional phosphorus retention, and areal hydraulic loading, which are then associated with the chlorophyll *a* and/or hypolimnetic dissolved oxygen (DO) concentrations (Brett and Benjamin, 2008; Cheng et al., 2010). Despite their successful application in predicting average whole-lake TP concentrations and DO levels in smaller inland lakes on the Canadian Shield (Dillon and Molot, 1996; Molot et al., 1992), these models have significant drawbacks when applied to larger systems. Namely, one of their

fundamental assumptions that the lake is thoroughly mixed with uniform concentrations throughout is profoundly violated in systems of larger size and complex shape whilst their capacity to predict the impact of episodic events (storm events, upwelling, climate change, and invasive species) is very limited.

An alternative to these empirical strategies has been the development of *process-based* models which can be used to understand ecological processes, to predict aquatic ecosystem responses to external nutrient loading changes, to evaluate management alternatives, and to support the policy making process (Jørgensen, 1997; Reckhow and Chapra, 1999). More than 40 years ago, Chen (1970) introduced a general model structure for addressing a broad class of water quality problems. This modelling framework essentially proposed a general set of ordinary or partial differential equations for describing key physical, chemical, and biological processes with site-specific parameters, initial conditions, and forcing functions, which were then used to reproduce real-world dynamics, to gain insights into the ecosystem functioning and to project future system response under significantly different external conditions (e.g., nutrient enrichment, climate change). The philosophy and the basic set of equations proposed in these early models still remain the core of the current generation of mechanistic aquatic biogeochemical models although advances in scientific understanding and improvements in methods of numerical analysis have

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brought significant progress with regard to the accuracy and sophistication. Reckhow and Chapra (1999) interpreted the fact that all the recent improvements in water quality modelling have built and evolved upon the foundation provided by early studies from the mid-70s as evidence of the strength of the original modelling propositions (Di Toro et al., 1971; Donigian and Crawford, 1976; O'Connor et al., 1975; Thomann et al., 1975). However, Arhonditsis et al. (2006) argued that the absence of novel ideas and creativity may also be a pathological symptom of the field of aquatic ecosystem modelling, inviting one to ask what it would take to prime the pump for significant breakthroughs to come along.

On a similar note, Arhonditsis and Brett (2004) attempted to evaluate the methodological consistency and general performance of 153 aquatic ecosystem modelling studies published in the international peer-reviewed literature between 1990 and 2002. Despite the heterogeneity of the selected papers with respect to model complexity, type of ecosystem modelled, spatial and temporal scales and model development objectives, this study reported a number of findings indicating that aquatic ecosystem modellers do not seem to consistently apply conventional methodological steps during the development of their models. The first striking feature of this analysis was the absence of systematic goodness-of-fit assessment of the original models (Fig. 1a). In the cases in which measures-of-fit or comparison plots were presented, Arhonditsis and Brett (2004) independently assessed state-variable performance as expressed by the relative error (RE) and the coefficient of determination (r^2) (Fig. 1b). Also the performance of existing mechanistic aquatic biogeochemical models was declined from physical-chemical to biological components of planktonic systems. The large majority of the published studies in the field over the last decade did not properly assess model sensitivity to the input vectors (Fig. 1c) whilst aquatic ecosystem modellers are still reluctant to embrace optimization techniques during model calibration, and assess the ability of their models to support predictions in the extrapolation domain (Fig. 1d). Thus, the establishment of a systematic methodological protocol for model assessment which is widely accepted by the aquatic biogeochemical modelling community should be a top priority. The modellers should understand that the methodological consistency is an analogue to the way a chemical analyst strives to attain clean laboratory conditions, excellent standardization curves, and faithful application of the analytical protocol. These methodological considerations will be some of the criteria for evaluating the rigour of eutrophication modelling in Lake Erie although the present study will place more emphasis on the implications of the parameterization of the existing models about the ecosystem characterization.

Eutrophication modelling in Lake Erie

Lake Erie is the smallest and shallowest system of the Great Lakes; and therefore, it is the most susceptible to nutrient-driven water quality issues. Recent evidence suggests that rapid ecological changes are in fact occurring in the ecosystem, involving a complex and often poorly understood interplay among many factors related to the lake's chemical, physical and biological characteristics (Michalak et al., 2013). A variety of aquatic biogeochemical models have been developed to understand ecological interactions and to predict the response of Lake Erie to external nutrient loading changes. Some of the models were constructed during the mid-1970s (e.g., Di Toro et al., 1987; Lam et al., 1987) whilst a new generation of models has been in place more recently (e.g., Leon et al., 2011; Zhang et al., 2008).

The evolution of eutrophication modelling should ideally follow the advancement of our understanding of the major causal linkages/ecosystem processes underlying the water quality problems in a particular system (Fig. 2). As such, the first type of models must be simple in structure and should revolve around the elucidation of the interplay among the exogenous nutrient loading,

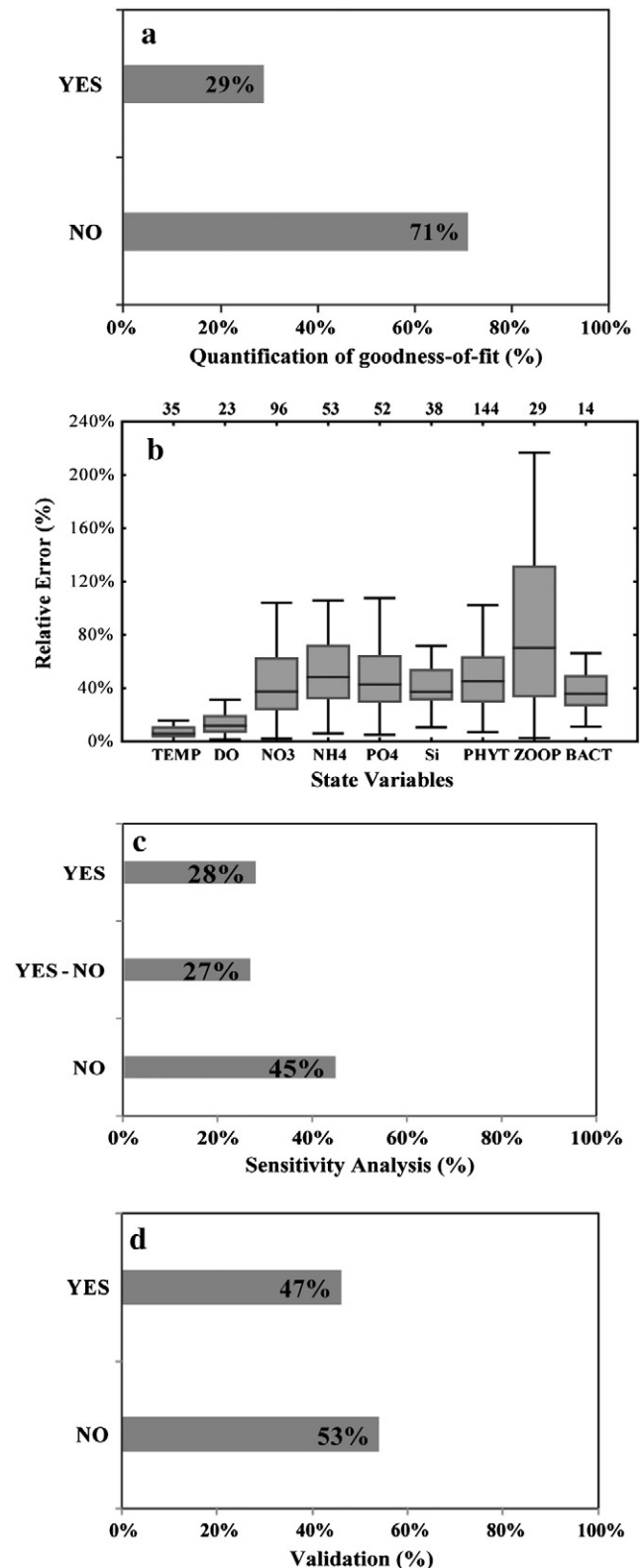


Fig. 1. (a) Percentage of modelling studies that quantified goodness-of-fit; (b) relative error (RE) of aquatic biogeochemical models for the study period 1990 to 2002 [number of studies assessed for each state variable is indicated on the top of the graph]; percentage of modelling studies that reported (c) sensitivity analysis; and (d) model validation. These figures are modified from Arhonditsis and Brett (2004).

ambient nutrient concentrations, and plankton dynamics. Whether statistical (data-driven) or mechanistic, the basic premise of these models is to capture effectively the direct signature of the abiotic forcing

on the lower food web variability with minimal consideration of the feedback loops (e.g., bacterial mineralization, internal loading) or the top-down control (e.g., planktivory). Our thesis is that if we do not have sufficient data to parameterize these simple causal linkages, it is unreasonable to expect that more complex (and profoundly over-parameterized) models will improve our predictive capacity! We should rather focus our efforts on optimizing the data collection efforts in this direction (e.g., error associated with the loading estimates) and solidify our understanding of the relative strength of the fundamental mechanisms of eutrophication in the study site of interest. When a narrowly defined model cannot adequately depict the eutrophication spatio-temporal patterns, we may then resort to the role of other potentially important driving factors, such as the capacity of the dominant residents of the benthic community (e.g., dreissenid mussels) or sediment diagenesis to modulate the dynamics of the littoral and (ultimately) the pelagic zone. Any additional complexity may be determined by the specific water quality issues (hypoxia, elevated toxin levels) of the studied ecosystem although modellers should explicitly recognize that this type of complex modelling constructs cannot be easily constrained by the available datasets; and as such, they are subject to considerable parametric and structural uncertainty (Denman, 2003; Pappenberger and Beven, 2006).

In this study, our primary objective is to evaluate the capacity of existing models in Lake Erie to depict the causal linkages between major water quality indicators (e.g., chlorophyll *a*, harmful algal blooms, dissolved oxygen) and nutrient loading. We first conducted a review of all the modelling efforts documented in the peer-reviewed literature (e.g., CE-QUAL-W2, ELCOM-CAEDYM), and then evaluated the performance of six models applied over the past thirty years (Table 1). The six models represent a wide range of temporal (daily, seasonal) resolutions and spatial scales (1-D, 2-D, 3-D). We examined the implications of the model parameterizations about the ecological processes underlying the plankton dynamics in Lake Erie and their ability to reproduce the spatial and temporal variability of hypoxia. Our goal was neither to vilify the modelling enterprise in Lake Erie nor to roundly criticize all the models developed. We recognize that a great deal of modelling work has been done to offer insights into the eutrophication processes in the system. Each of the models examined has advantages and disadvantages and our aim with the present study was to impartially identify them. Finally, our study discusses the future augmentations of Lake Erie modelling, i.e., which are the most appropriate (and feasible) models to address questions related to

hypoxia and cyanobacteria dominance, and the data that necessitate to ground-truth those models.

Lake Erie eutrophication model by Di Toro and Connolly (1980)

The Lake Erie eutrophication model by Di Toro and Connolly (1980) represents one of the first attempts to use complex mechanistic modelling for guiding the decision making process in the Great Lakes area. The model was used to estimate the reduction in phosphorus loading required to meet the International Joint Commission (IJC) objective of anoxia elimination in the central basin (Di Toro et al., 1987). The model comprises a set of mass balance equations which quantify the mass transport and kinetic interactions of five elemental cycles (phosphorus, nitrogen, silica, carbon and oxygen) with the planktonic food web (Electronic Supplemental Material (ESM) Fig. SI-1). In particular, the model considers two phytoplankton (diatoms and non-diatoms) and two zooplankton (herbivores and carnivores) functional groups. The fifteen state variables of the model are reported in Table 1. The spatial segmentation of the model divides Lake Erie into six compartments, representing the epilimnia and hypolimnia of the western, central, and eastern basins, and three underlying active sediment layers.

The original calibration of the model was based on data from the 1970 and the 1973–1974 survey years (Di Toro and Connolly, 1980). The parameter specification of the Lake Erie model resembled those reported for the Lake Ontario and Lake Huron/Saginaw Bay models (Di Toro and Matystik, 1979; Thomann et al., 1975), whilst the site-specific adjustments mainly involved the growth and kinetic constants of the phytoplankton and zooplankton functional groups. Notably, Di Toro and Connolly (1980) presented a detailed justification of the parameter values assigned after a meticulous review of the available literature at that time. The first verification (or predictive validation) of the model was based on data from 1975; a year that was not really suitable to examine model performance in the extrapolation domain because the phytoplankton and nutrient concentrations in 1975 were approximately the same as in the years 1970–1974. Nonetheless, the central basin of Lake Erie in that year did not become anoxic; and therefore, it offered an excellent opportunity to examine the capacity of the model to reproduce oxygen conditions significantly different from those used during its calibration. The comparison between calibration and verification error indicated that the model residuals were approximately 50% larger for the model validation than the training exercise (Di Toro and Connolly, 1980); a result that is frequently

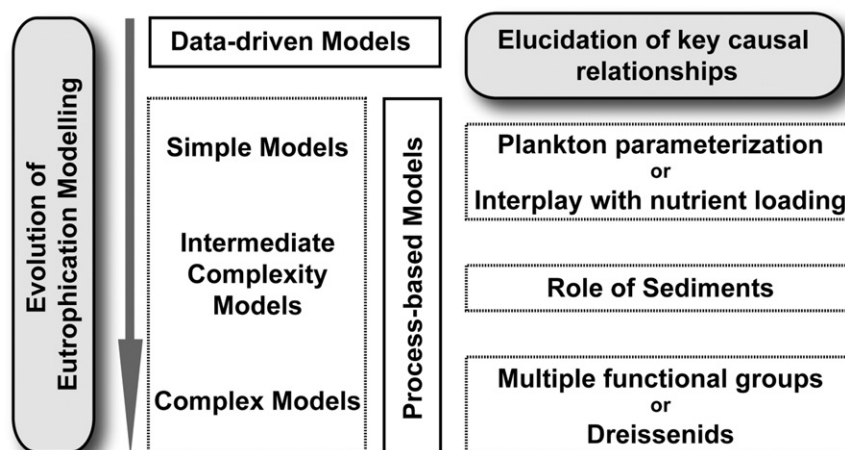


Fig. 2. Conceptual diagram illustrating the evolution of modelling across different levels of structural and functional complexity in response to our understanding of the eutrophication problems in a studied system. The first type of models must be simple in structure, statistical or simple mechanistic, and they should focus on the elucidation of the interplay among the exogenous nutrient loading, ambient nutrient concentrations, and plankton dynamics. If this narrowly defined system cannot adequately depict the eutrophication spatio-temporal patterns, we should then resort to the role of other potentially important driving factors, such as the capacity of the dominant residents of the benthic community (e.g., dreissenid mussels) or sediment diagenesis to modulate the dynamics of the littoral and ultimately the pelagic zone.

Table 1
Six eutrophication models developed to represent the causal linkages among nutrient loading, phytoplankton dynamics, and hypoxia patterns in Lake Erie.

Criteria	Di Toro et al. (1987)	Rucinski et al. (2010)	Zhang et al. (2008)	Leon et al. (2011)	Stumpf et al. (2012)	Zhou et al. (2013)
Short description	Multiple-box model	1-D DO model coupled with POM	2-D CE-QUAL-W2 model	3-D coupled ELCOM-CAEDYM	Cyanobacterial Index (CI) – phosphorus loading empirical model	Universal Kriging and conditional realizations of hypoxic extent
Spatial configuration	Six (6) water segments and four (4) sediment segments representing the western, central and eastern basins	48 vertical layers in central basin	65 vertical layers at 1 m intervals and 222 longitudinal segments from west to east	2 km grid with 40 vertical layers	Western basin	Estimates of the hypoxia extent in the central basin of Lake Erie
Temporal domain	Daily resolution Calibration (1970, 1973–1974) Post-auditing (1970–1980)	Daily resolution Calibration (1987–2005)	Daily resolution (May–September) Calibration (1997) Verification (1998 and 1999)	Hourly averages 190 days in 2002 (mid-April to mid-October)	Cyanobacterial Index against monthly or seasonal flow discharge/P loading Calibration (2002–2011)	Summer DO distribution from 1987 to 2007
Model outputs/state variables	<i>Phytoplankton (chlorophyll a)</i> : Diatoms, non-diatoms <i>Zooplankton (carbon)</i> : Herbivores, carnivores <i>Nutrients</i> : Detrital and dissolved organic nitrogen, ammonia, nitrate, unavailable phosphorus, soluble reactive phosphorus, unavailable silica, soluble reactive silica, detrital organic carbon, dissolved inorganic carbon, alkalinity, dissolved oxygen	Water temperature Dissolved oxygen	<i>Phytoplankton</i> : Non-diatom edible algae, non-diatom inedible algae, diatoms <i>Zooplankton</i> : Cladocerans, copepods (eggs, nauplii, copepodites, adults) <i>Nutrients</i> : Nitrate, ammonium, phosphate, carbon dioxide, soluble reactive silica, labile dissolved organic matter, particulate silica, dissolved oxygen Dreissenid mussels are included as external forcing (grazing and nutrient excretion)	Biomass of the five phytoplankton functional groups modelled, intracellular N and P storage, dissolved inorganic nutrients (PO ₄ , NO ₃ , NH ₄ , DIC, and RSi), dissolved organic (DOC, DON, and DOP) and particulate detrital organic matter groups (POC, PON, and POP), inorganic suspended solids size classes, and dissolved oxygen	Cyanobacterial Index (CI) was calculated by using the spectral shape around the 681 nm band. The spectral shape is determined as a nominal second derivative around the band of interest (681 nm, 709 nm, and 665 nm). Using the individual CI images, 10-day composites were calculated by taking the highest CI at each pixel available from any of the daily images within a given 10-day time period.	Hypoxic extent of Lake Erie

reported in the modelling literature (Chapra, 1997; Jørgensen and Bendoricchio, 2001).

A follow-up analysis by Di Toro et al. (1987) offered a more rigorous evaluation of the predictive capacity of the model to reproduce the interplay among nutrients, plankton dynamics, and dissolved oxygen over a 10-yr period (1970–1980). Although the Di Toro et al. (1987) study did not report goodness-of-fit statistics from the long-term simulations, it was argued that the model had the capability to sufficiently reproduce the observed water quality improvements and decrease hypoxia patterns in response to exogenous phosphorus loading reductions. However, a careful visual inspection of the presented results suggests to us that the model actually failed to reproduce the intra-annual total and soluble reactive phosphorus (SRP) variability (see their Fig. 9), to faithfully depict the year-to-year variability of algal dynamics (see their Fig. 10), and to capture the long-term nitrate trends in Lake Erie (see their Fig. 12). The authors of the study partly attributed the model misfit to the inadequate characterization of certain processes (e.g., sediment denitrification) and/or the error associated with observed data and forcing functions (Di Toro et al., 1987). Nevertheless, we believe that the lack of sensitivity/uncertainty analysis, and not the model error itself, was the major impediment of that modelling study to guide water quality management decisions and formulate risk assessment statements. From a management standpoint, our thesis is that significantly more information is conveyed when the model uncertainty and the potential causes for the misrepresentation of the system are combined with the mean predictions. In doing so, the predictive statements impartially communicate both what a model can actually deliver and our level of confidence when basing ecological forecasts upon it (Beven and Alcock, 2012; see also following discussion).

A simple one-dimensional, climate-based dissolved oxygen model for the central basin of Lake Erie by Rucinski et al. (2010)

The Rucinski et al. (2010) study presented a one-dimensional coupled thermal budget-dissolved oxygen model to examine the inter-annual variability in dissolved oxygen dynamics in the central basin of Lake Erie, and to evaluate the causal association between that variability and climate-driven mixing and temperature regimes. The physical model used was based on a 1-D version of the Princeton Ocean Model (POM), which in turn is founded upon a two-equation Mellor–Yamada turbulence model for vertical diffusivity (Mellor, 2001). POM separated the lake into 48 vertical layers of 0.5 m each, and the model was calibrated with temperature observations from 1994 in central Lake Erie. The root-mean-squared-error (RMSE) values were ranging between 0.5 and 1.7 °C whilst the highest error was associated with the representation of the thermocline temperatures (below 17 m). Overall, the 1-D model accurately described the onset of stratification and thermocline development in summer, but it failed to reproduce the increase in the mixed layer depth caused by storms towards the late August and early September. The latter problem was attributed to three dimensional hydrodynamic processes, such as horizontal advection and internal wave propagation, unaccounted for by the one dimensional representation of the system.

The dissolved oxygen sub-model simulates the vertical profiles of dissolved oxygen with a coupled set of differential mass balance equations in the 48 model segments (ESM Fig. SI-2). The bulk oxygen dynamics (i.e., the combined effects of photosynthesis, respiration, decomposition) in each layer were determined by the mixing rates between the vertical layers and a first-order, temperature-corrected deoxygenation rate, the so-called water column oxygen demand (WCOD) which was the only calibration parameter of the model. The WCOD was applied below the thermocline, where respiration is greater than photosynthesis, whilst the well-mixed epilimnion was predominantly impacted by the prevailing boundary conditions at the lake surface–atmosphere interface. Additionally, the model considered a temporally

constant areal flux to the bottom segment, accounting for the role of the sediment oxygen demand (SOD). The model was calibrated for 1987–2005 by assigning year-specific WCOD values to match the observed timing of the onset of hypoxia, and to subsequently examine how oxygen demand varied among years. Although the Rucinski et al. (2010) study did not report a rigorous goodness-of-fit for the DO simulations, it was noted that the magnitude and timing of the oxygen minima were captured fairly well. There were discrepancies between modelled and observed DO concentrations at the thermocline that likely stemmed from the aforementioned limitations of the thermal model. Importantly, the model results suggested that WCOD can demonstrate significant interannual variability. Specifically, the water column oxygen demand in the Central Basin of Lake Erie changed significantly between 1987 and 2005, with higher depletion rates early, declining to a minimum in 1993, followed by an increase from 1994 to 2005. WCOD values were found to have a weak relationship with the thermal properties, but there was a distinct pattern of covariance with soluble reactive phosphorus loading. Namely, soluble reactive phosphorus loads followed a similar increasing trend from 1994 to 2005, stemming from demographic changes, altered agricultural practices (e.g., conservation tillage) and animal density. Because the soluble reactive phosphorus inflows directly stimulate the primary production, they are likely to be the dominant drivers of hypoxia since the mid-1990s relative to changes in climate. In this regard, the Rucinski et al. (2010) thermal budget-dissolved oxygen model offered a much needed heuristic tool to elucidate a key causal link in Lake Erie. However, the fact that the WCOD was not treated as a model endpoint, but rather as an adjustable input parameter, suggests that we cannot really forecast through the model the capacity of nutrient loadings to modulate hypoxia patterns. The model could be predictive only if an empirical relationship among WCOD, SRP loads and/or other meaningful covariates is established.

A two-dimensional ecological model of Lake Erie: application to estimate dreissenid impacts on large lake plankton populations by Zhang et al. (2008)

The Zhang et al. (2008) study presented a two-dimensional ecological model that was used to elucidate potentially important ecosystem processes in Lake Erie, such as the algal succession, the food competition between dreissenids and zooplankton, and the contribution of internal relative to external phosphorus loading. The model configuration divides Lake Erie into 65 vertical layers at 1 m intervals and 222 longitudinal segments from west to east. The physical component was based on the CE-QUAL-W2, a two-dimensional, longitudinal and vertical, hydrodynamic model that accurately depicted the variability of water levels, water currents, and thermal stratification in the system (Boegman et al., 2008; Cole and Buchak, 1995). The ecological model includes three phytoplankton and two zooplankton functional groups: non-diatom edible algae (NDEA), non-diatom inedible algae (NDIA), diatoms, cladocerans and copepods. Interestingly, the dreissenid mussels are not included as a state variable, but rather their role is considered as external grazing and nutrient excretion forcing (ESM Fig. SI-3).

The simulation of the algal growth rate (μ) was based on assumption that the maximum growth rate (μ_{\max}) is affected by temperature, light, and nutrient availability (Table 2):

$$\mu = \mu_{\max} f(T) f(\text{NI})$$

$$f(\text{NI}) = \min[f(\text{N}), f(\text{P}), f(\text{I}), f(\text{Si})]$$
(1)

where $f(T)$ is temperature rate multiplier and $f(\text{NI})$ is a multiplier that accounts for the growth limitation posed by light and nutrients. Diatoms were assumed to have the lowest optimum temperature range, whilst a higher optimum temperature range was assigned to NDIA algae relative to NDEA. Nitrogen, phosphorus and silicon (diatoms) were the limiting

Table 2
The phytoplankton characterization of two mechanistic eutrophication models in Lake Erie.

	Zhang et al. (2008)	Leon et al. (2011)
Phytoplankton functional groups	Non-diatom edible algae (NDEA) Non-diatom inedible algae (NDIA) Diatoms (D)	Early diatoms (ED) Late diatoms (LD) Cyanophytes (C) Flagellates (F) Other phytoplankton (O)
Intracellular N and P	Constant	Dynamic
<i>Mathematical processes</i>		
Phytoplankton growth limitation	$\mu = \mu_{\max} f(T) \min[f(N), f(P), f(I), f(Si)]$	$\mu = \mu_{\max} f(T) \min[f(N), f(P), f(I), f(Si)]$
Temperature limitation	If T varies within optimal temperature ranges ($T_1 \leq T \leq T_4$): $f(T) = \frac{K_1 e^{\gamma_1 (T-T_1)}}{1 + K_1 e^{\gamma_1 (T-T_1)} - K_1} \frac{K_4 e^{\gamma_2 (T_4-T)}}{1 + K_4 e^{\gamma_2 (T_4-T)} - K_4}$ where $\gamma_1 = \frac{1}{T_2 - T_1} \ln \frac{K_2(1-K_1)}{K_1(1-K_2)}$ $\gamma_2 = \frac{1}{T_4 - T_3} \ln \frac{K_3(1-K_4)}{K_4(1-K_3)}$ else: $f(T) = 0$	$f(T) = \vartheta^{T-20} + \vartheta^{C1(T-C2)} + C3$ where $C1, C2$ and $C3$ are constants at $T = T_{STD}$, $f(T) = 1$ at $T = T_{OPT}$, $\partial f(T) / \partial t = 0$ at $T = T_{MAX}$, $f(T) = 0$
Light limitation	$f(I) = \frac{1}{I_k} \exp\left(1 - \frac{I}{I_k}\right)$	$f(I) = 1 - \exp\left(-\frac{I}{I_k}\right)$
Phosphorus limitation or uptake	$f(P) = \frac{PO_4}{PO_4 + K_{PO4}}$	$U_{PO4} = U_{P_{MAX}} \left[\frac{IP_{MAX} - IP_{INT}}{IP_{MAX} - IP_{MIN}} \frac{PO_4}{PO_4 + K_{PO4}} \right]$
Nitrogen limitation or uptake	$f(N) = \frac{IN}{IN + K_{NH4}}$	$U_{NH4} = P_N U_{N_{MAX}} \left[\frac{IN_{MAX} - IN_{INT}}{IN_{MAX} - IN_{MIN}} \frac{IN}{IN + K_{NH4}} \right]$ $U_{NO3} = (1 - P_N) U_{N_{MAX}} \left[\frac{IN_{MAX} - IN_{INT}}{IN_{MAX} - IN_{MIN}} \frac{IN}{IN + K_{NH4}} \right]$
Silica limitation	$f(Si) = \frac{Si}{Si + K_{Si}}$	$f(Si) = \frac{Si}{Si + K_{Si}}$
Ammonium preference	$P_N = \left[\frac{NH_4 \cdot NO_3}{(NH_4 + K_{NH4})(NO_3 + K_{NH4})} \right] + \left[\frac{NH_4 \cdot K_{NH4}}{(NH_4 + NO_3)(NO_3 + K_{NH4})} \right]$	$P_N = \left[\frac{NH_4 \cdot NO_3}{(NH_4 + K_{NH4})(NO_3 + K_{NH4})} \right] + \left[\frac{NH_4 \cdot K_{NH4}}{(NH_4 + NO_3)(NO_3 + K_{NH4})} \right]$
Algal losses (respiration, excretion, mortality)	$R = \gamma_1 k_{ar \max} + (1 - f(I)) k_{ae \max} + \gamma_1 k_{am \max}$	$R = k_R \vartheta_R^{(T-20)}$

nutrients, and their role on algal growth was accounted for by a Monod relationship. The latter expression postulates that the nutrient composition of the algal cells remains constant and the ambient nutrient concentrations are directly linked to the algal growth rates (Table 2). Whilst the algal growth submodel is far from novel, we caution that the decision to include light limitation within Liebig's Law of the Minimum may be problematic, as it was essentially postulated that there is one single factor that limits the phytoplankton growth, and thus there is no interplay between light and nutrients. Moreover, because of the parameter values assigned during the model calibration, it is very likely that the role of light availability may have been overstated as the predominant factor that shapes the competition patterns among the phytoplankton functional groups considered (see also following discussion). Importantly, these model specifications appear to contradict empirical evidence that an intricate resource competition for water temperature, irradiance, and nutrient (nitrogen, phosphorus, silicon) availability determines the abundance and composition of the algal assemblage in Lake Erie (Allinger and Reavie, 2013; Millie et al., 2009). Thus, the consideration of a multiplicative mathematical formulation that explicitly accommodates the interplay between light and nutrients would have been a more appropriate choice. In addition, given the low summer epilimnetic phosphate levels (<5 µg/L), we believe that a two-step algal growth submodel which first considers the nutrient uptake rate in relation to the ambient supply and subsequently the growth rate as a function of the internal nutrient storage is more suitable. There is abundant evidence in the literature that the intracellular storage strategies are likely another important factor that shapes the inter-specific competition and consequently the dynamics of the epilimnetic phytoplankton communities in both simulated environments and "real world" settings (Sommer, 1991; Zhao et al., 2008).

Another interesting feature of the Zhang et al. (2008) study was the stage-structured population model for copepod biomass (Fennel and Neumann, 2003) and the general mass conservation model for the

population of cladocerans (Scavia et al., 1988). The former submodel consisted of four biomass state variables for copepod eggs, nauplii, copepodites, and adults. The representation of zooplankton was certainly novel and ecologically more realistic, which in turn may provide greater constraint to the parameters by enabling to draw upon empirical studies of zooplankton reported in the literature. That is, when the model parameters are specified to resemble quantities that can be measured in the real world, i.e., group/life stage-specific (instead of generic) physiological characteristics or biological rates, then the increased model complexity is not necessarily an impediment to characterizing the modelled processes. On the other hand, if the relevant information is not available, the increased disparity between what we want to tease out from the model and what can be pragmatically studied in the real system could conceivably inflate the model uncertainty and thus pose limitations on its use for predictive purposes (Denman, 2003; Reichert and Omlin, 1997).

The calibration of the model was based on data from 1997, whilst the (practically similar in terms of system dynamics) 1998–1999 survey period was used for model verification. Among the 54 cases examined (6 state variables × 3 years × 3 basins), paired t-tests showed that modelled values and field measurements did not differ in 38 cases and were significantly different in 16 instances. Diatom biomass was the state variable with the highest number (8) of cases with no (statistical) difference between observed data and modelled outputs, whilst copepods and total dissolved phosphorus showed the lowest number (5) of non-significant differences. Further, the median relative error (MRE) values were below 50% for all six state variables in the three years simulated.

Although the performance of the model was encouraging, the authors pointed out that the model is more suitable to be considered as a valid analytical/heuristic tool rather than a predictive device to support ecosystem forecasts. To this end, Zhang et al. (2008) examined two ecological hypotheses: (i) dreissenid grazing impacts on algal

groups are highly constrained by the boundary layer above the mussel bed, where phytoplankton biomass is low relative to the upper waters so that even a large mussel population would not depress the phytoplankton community in Lake Erie; (ii) dreissenid nutrient excretion has a greater role in algal succession than does their grazing, especially when the mussel population is large. The model results suggested that dreissenid grazing impacts on NDEA are weakened by the boundary layer above the basin bottom. On the other hand, dreissenid grazing impacts on diatoms are less affected by the boundary layer due to the higher sinking rates of diatoms. NDIA increase rapidly with an increasing mussel population size, given that the dreissenids excrete a large amount of ammonia and phosphate. The authors also concluded that dreissenid mussels have weak direct grazing impacts on algal biomass, whilst the indirect effects of their nutrient excretion may have a greater impact on the system. Finally, we note that the 2-D spatial segmentation of the Zhang et al. (2008) model disallows the simulation of the nearshore–offshore gradients, whilst the fact that dreissenids are effectively treated as a forcing function impedes the use of the model for predictive purposes.

Application of a 3D hydrodynamic–biological model for seasonal and spatial dynamics of water quality and phytoplankton in Lake Erie by Leon et al. (2011)

Leon et al. (2011) presented a three-dimensional (3-D) coupled hydrodynamic–biological model that was used to capture the temporal and spatial variability of phytoplankton and nutrients in Lake Erie. The Estuary, Lake and Coastal Ocean Model (ELCOM) was applied to simulate the physical and transport processes in the water body, whilst the Computational Aquatic Ecosystem Dynamics Model (CAEDYM) formed the basis to simulate the C, N, P, DO, and Si cycles, along with inorganic suspended solids and phytoplankton. The bathymetry was set up on a 2 km grid with 40 vertical layers, and the simulation period was

190 days (mid–April to mid–October) for 2002. The ELCOM–CAEDYM model dynamically calculated the following state variables: algal biomass, the intracellular N and P storage, five dissolved inorganic nutrients (PO_4 , NO_3 , NH_4 , DIC, and RSi), three dissolved organic (DOC, DON, and DOP), three particulate detrital organic matter forms (POC, PON, and POP), two inorganic suspended solid size classes (SS1 and SS2), and dissolved oxygen (DO) (ESM Fig. SI-4).

Leon et al. (2011) aimed to reproduce the seasonal succession patterns of the Lake Erie algal assemblage by considering five phytoplankton functional groups: (i) the “early diatoms” group representing the early-blooming diatom taxa with high Si requirements and rapid sinking rates; (ii) the “late diatoms” group representing the diatoms with lower Si requirements and sinking rates that occur later in the seasonal succession (also include some of the silicified chrysophytes); (iii) a “cyanophyte” group mainly defined as the larger and potentially N-fixing taxa that are often associated with warm and stable waters; (iv) the “flagellates” corresponded to cryptophytes and other flagellates typical of cooler waters and/or deeper strata (also include some non-motile forms that have similar preferences and low sinking rates, e.g. some picocyanobacteria); and (v) the “other phytoplankton” group representing the flagellates and non-motile forms that are typical of warmer and brighter conditions (e.g., many chlorophytes and some dinoflagellates, chrysophytes, and haptophytes).

Maximum potential growth rates (gross photosynthesis), losses to respiration, excretion and mortality, and the difference between settling and re-suspension rates were used to characterize the different phytoplankton groups (Table 3). Group-specific algal growth rates were reproduced by a mathematical expression similar to Zhang et al. (2008), determined by a maximum growth rate at reference temperature as modified by a temperature rate multiplier and Liebig's Law of the Minimum for light, P, N and Si limitation (Eq. (1)). The authors noted that the P half saturation constants were similar for all the

Table 3

Comparison of the parameter values assigned to the phytoplankton functional groups of the Zhang et al. (2008) and Leon et al. (2011) eutrophication models in Lake Erie.

Phytoplankton functional groups ^a	Zhang et al. (2008)			Leon et al. (2011)					
	NDEA	NDIA	D	ED	LD	C	F	O	
Settling velocity (m d^{-1})	v	0.05	0.05	0.2	0.09	0.09	0.07	0.02	0.02
Maximum growth rates (d^{-1})	μ_{max}	3.0	2.0	3.0	1.7	1.9	0.8	0.8	1.0
Temperature coefficient for growth	θ	N/A	N/A	N/A	1.048	1.075	1.09	1.06	1.06
Half saturation constant for PO_4 (mg P L^{-1})	K_{PO_4}	0.002	0.01	0.002	0.009	0.006	0.009	0.003	0.003
Half saturation constant for NH_4 (mg N L^{-1})	K_{NH_4}	0.03	0.001	0.03	0.045	0.045	0.045	0.045	0.06
Half saturation constant for silica ($\text{mg SiO}_2 \text{ L}^{-1}$)	K_{Si}	N/A	N/A	0.03	0.150	0.055	N/A	N/A	N/A
Maximum internal P concentration (mg P mg Chla^{-1})	IP_{MAX}	N/A	N/A	N/A	1.8	1.3	1.0	1.0	2.0
Minimum internal P concentration (mg P mg Chla^{-1})	IP_{MIN}	N/A	N/A	N/A	0.18	0.13	0.1	0.1	0.3
Maximum internal N concentration (mg N mg Chla^{-1})	IN_{MAX}	N/A	N/A	N/A	4.0	4.0	4.0	9.0	4.0
Minimum internal N concentration (mg N mg Chla^{-1})	IN_{MIN}	N/A	N/A	N/A	2.0	2.0	2.0	3.0	2.0
Maximum P uptake rate ($\text{mg P mg Chla}^{-1} \text{ d}^{-1}$)	UP_{MAX}	N/A	N/A	N/A	0.4	1.0	1.0	0.7	2.0
Maximum N uptake rate ($\text{mg N mg Chla}^{-1} \text{ d}^{-1}$)	UN_{MAX}	N/A	N/A	N/A	1.5	1.5	1.5	1.5	1.5
Saturation light intensity of photosynthesis (W m^{-2})	I_k	120	50	120	13	13	29	9	22
Standard temperature for algal growth ($^{\circ}\text{C}$) where $f(T) = 1.0$	T_{STD}	N/A	N/A	N/A	7	19	24	19	24
Optimum temperature for algal growth ($^{\circ}\text{C}$) where $f(T) = \text{maximum}$	T_{OPT}	N/A	N/A	N/A	9.8	23	30	21	29
Maximum temperature for algal growth ($^{\circ}\text{C}$) where $f(T) = 0$	T_{MAX}	N/A	N/A	N/A	18.5	31	39	27.5	35
Lower temperature for growth ($^{\circ}\text{C}$)	T_1	4	15	4	N/A	N/A	N/A	N/A	N/A
Lower temperature for maximum growth ($^{\circ}\text{C}$)	T_2	18	22	12	N/A	N/A	N/A	N/A	N/A
Upper temperature for maximum growth ($^{\circ}\text{C}$)	T_3	25	30	16	N/A	N/A	N/A	N/A	N/A
Upper temperature for growth ($^{\circ}\text{C}$)	T_4	35	35	35	N/A	N/A	N/A	N/A	N/A
Coefficient representing temperature effect on growth at T_1	K_1	0.10	0.10	0.10	N/A	N/A	N/A	N/A	N/A
Coefficient representing temperature effect on growth at T_2	K_2	0.99	0.99	0.99	N/A	N/A	N/A	N/A	N/A
Coefficient representing temperature effect on growth at T_3	K_3	0.99	0.99	0.99	N/A	N/A	N/A	N/A	N/A
Coefficient representing temperature effect on growth at T_4	K_4	0.10	0.10	0.10	N/A	N/A	N/A	N/A	N/A
Algal respiration rate (d^{-1})	$k_{\text{ar max}} (k_R)$	0.05	0.05	0.05	0.13	0.15	0.17	0.2	0.11
Algal excretion rate (d^{-1})	$k_{\text{ae max}}$	0.01	0.04	0.01					
Algal mortality rate (d^{-1})	$k_{\text{am max}}$	0.07	0.03	0.07					
Temperature coefficient for respiration	θ_R	N/A	N/A	N/A	1.09	1.035	1.06	1.08	1.08
Detritus settling rate (d^{-1})	v_{DET}	0.5							
Detritus decay rate (d^{-1})	$K_{\text{d DET}}$	0.08							
Ammonium decay rate (d^{-1})	$K_{\text{d NH}_4}$	0.12							
Nitrate decay rate (d^{-1})	$K_{\text{d NO}_3}$	0.05							

^a Abbreviations of phytoplankton functional groups are provided in Table 2.

phytoplankton functional groups except from “cyanobacteria”, which were associated with a higher value. However, in their Appendix C, both “cyanobacteria” and “early diatoms” had the highest P half saturation constants ($0.009 \text{ mg P L}^{-1}$), the “late diatoms” were assigned a value of $0.006 \text{ mg P L}^{-1}$, whilst “flagellates” and “other phytoplankton” groups were characterized by superior P kinetics, i.e., $0.003 \text{ mg P L}^{-1}$ (Table 3). Aside from the “other phytoplankton” group, the values assigned to the group-specific N half saturation constants were similar because the authors asserted that the N kinetics are unlikely to have a strong influence on phytoplankton dynamics due to fairly high levels of inorganic nitrogen ($>0.2 \text{ mg N L}^{-1}$) in Lake Erie.

Model predictions were compared against measurements of epilimnetic Chla and TP by using coefficients of determination (r^2). Observations could differ markedly from model predictions for individual stations and dates (in log–log plots, $r^2 = 0.48$ for Chla; and $r^2 = 0.40$ for TP). The authors found that the major systematic bias demonstrated by the ELCOM–CAEDYM model was a TP overestimation during the summer stratified season in the east and central basin. According to the authors’ of the study, this result may have stemmed from incorrect assumptions about the fraction of non-bioavailable (apatite) P in external loading, which seems to be higher than what was assumed in the tributary loads. The authors claimed that the model predictions of phytoplankton succession were reasonable, as the predicted dominance of “early diatoms” in the spring phytoplankton maximum was on par with existing empirical knowledge. The “cyanobacteria” group was predicted to remain a small fraction of the phytoplankton biomass, despite the known occurrence of cyanobacterial outbreaks in the western basin. Nonetheless, it was argued that these blooms tend to be episodic and spatially limited events whilst the available data support the model predictions of a normally low cyanobacterial contribution to biomass. Regarding the performance of the ELCOM–CAEDYM model, Leon et al. (2011) noted that the uncertainty associated with the exogenous loading forcing could be an important underlying factor. However, although one of their main objectives was the relative contribution of the localized nutrient inputs to the phytoplankton abundance in nearshore areas, the study did not report a rigorous assessment of the broad range of system dynamics that can be induced when we account for the uncertainty of the intra- and interannual loading estimates. Also, there was no sensitivity analysis of the ecological characterization; an essential exercise that can identify the most influential parameters to the model outputs and thus dictate the kind of data needed to validate the model.

The model calibration was rationalized as “a portrayal of the interactions between physical processes (hydrodynamics, temperature and irradiance variations) and a relatively simple, but defensible, set of assumptions concerning the ecological processes of interest”, but the practice followed implicitly postulated a predominance of the physical transportation over the biological processes. The importance of the mesoscale physical processes in shaping the spatiotemporal patterns of biotic communities is unquestionable. There are also instances where the spatial structure is necessary for the correct parameterization of a process-based model, as a “box” configuration would produce parameters that may not be useable in a spatially structured model. However, the planktonic dynamics should be reasonably reproduced prior to the integration with the circulation model. That is, rather than selecting general literature values and/or tuning some biological parameters (e.g., growth rates and kinetics) whilst the hydrodynamic model is active, it would have been interesting to undertake an independent calibration of the ecological model and then integrate the two models. Given that the algal seasonal succession patterns are sensitive and are only manifested in a narrow region of the parameter space (Zhao et al., 2008), many of the plankton patterns presented by Leon et al. (2011) would have disappeared if the same ecological parameter specification was implemented in a simpler spatial structure. The same exercise may also allow handling more properly the model spin-up, and thus overcoming the limitations posed by the computationally demanding 3-D simulations. Finally, it is also interesting to note that this practice has been adopted several times in the

context of Great Lakes modelling although oceanic modellers typically follow the aforementioned two-step approach, i.e., they calibrate the plankton models within a simple spatial (single-box) configuration and then let the hydrodynamics accommodate the spatial variability that is not captured by the “box model” parameters. A characteristic example is the advancement of the original coarse resolution of the Fasham et al. (1990) model to the spatially refined presentations of the limiting nutrient–phytoplankton–zooplankton–detritus (NPZD) model (Doron et al., 2011; Mattem et al., 2010; Popova et al., 2002).

Interannual variability of cyanobacterial blooms in Lake Erie by Stumpf et al. (2012)

Stumpf et al. (2012) presented an empirical regression model to predict the likelihood of cyanobacteria blooms as a function of the average discharge (Q) of Maumee River between March and June and the total phosphorus (TP) concentrations in June. Medium-spectral Resolution Imaging Spectrometer (MERIS) imagery was used to quantify intensity of the cyanobacterial blooms for each year from 2002 to 2011. The Cyanobacterial Index (CI) was calculated by using the spectral shape (SS) around the 681 nm band, $CI = -SS(681)$. The spectral shape (SS) is determined as a nominal second derivative around the band of interest (681 nm, 709 nm, and 665 nm). Using the individual CI images, 10-day composites were calculated by taking the highest CI at each pixel available from any of the daily images within a given 10-day time period to remove clouds and capture the areal biomass (each year has 15 CI composites, from June 1–10 to October 19–28). The latter step was followed because *Microcystis* typically aggregates at the surface providing effective detection with remote sensing. Time series of bloom intensity showed that the intense cyanobacteria blooms typically last 30–40 days and sometimes can even be up to a few months. The peaks of cyanobacteria blooms occurred in August, September, and once in early October (2011), whilst the annual bloom severity was determined by averaging the highest three consecutive 10-day composites. River discharge (Q) was monthly averaged from the daily discharge averages of Maumee River whilst the monthly phosphorus and nitrogen loadings were calculated from daily loads using flow-weighted concentrations in the USGS Maumee River gage station.

The Cyanobacterial Index was regressed against temperature, river discharge, nitrogen, TP, and SRP loading using least squares fitting, and the corresponding p-values along with the residual standard error (RSE) were used to determine significance of the models. The study indicated that interannual differences in summer temperatures cannot explain the variations in bloom intensity. Nitrogen (NOx) loads also do not exert a significant control on bloom intensity. The annual CI demonstrated statistically significant relationships with single month river discharges and phosphorus loading in the spring (March, April, and May) (r^2 from 0.09 to 0.55). June had a unique pattern between CI and nutrient loads, in that it was strongly associated with TP, when 2004 and 2011 were excluded ($r^2 = 0.91$) (Fig. 3a). The r^2 value of the linear regression model further increased when CI was regressed against the cumulative load for sequential months, e.g., from March to May. When June was added to the March to May totals, TP and Q explained 89% and 97% of the CI variance in bloom years (Fig. 3d). Among the six bloom years, spring Q produced a stronger relationship to bloom intensity than TP or SRP loading (Figs. 3b, c). Spring TP also showed a strong relationship ($r^2 = 0.89$), although the RSE value was higher (Fig. 3b). Interestingly, the exponential model for CI against Q resulted in the same $r^2 = 0.97$, but RSE was improved (Fig. 3d).

These empirical models are certainly essential in advancing our understanding of the key drivers of cyanobacteria dominance, but the relatively small sample size ($n = 10$) used for their derivation may be an impediment for their forecast performance and broader application. For example, two data points (2004 and 2011) had to be removed from the CI vs. TP_{June} model in order to improve the relationship. Another good fitting model (CI vs. Q_{March–June}) was solely populated by bloom

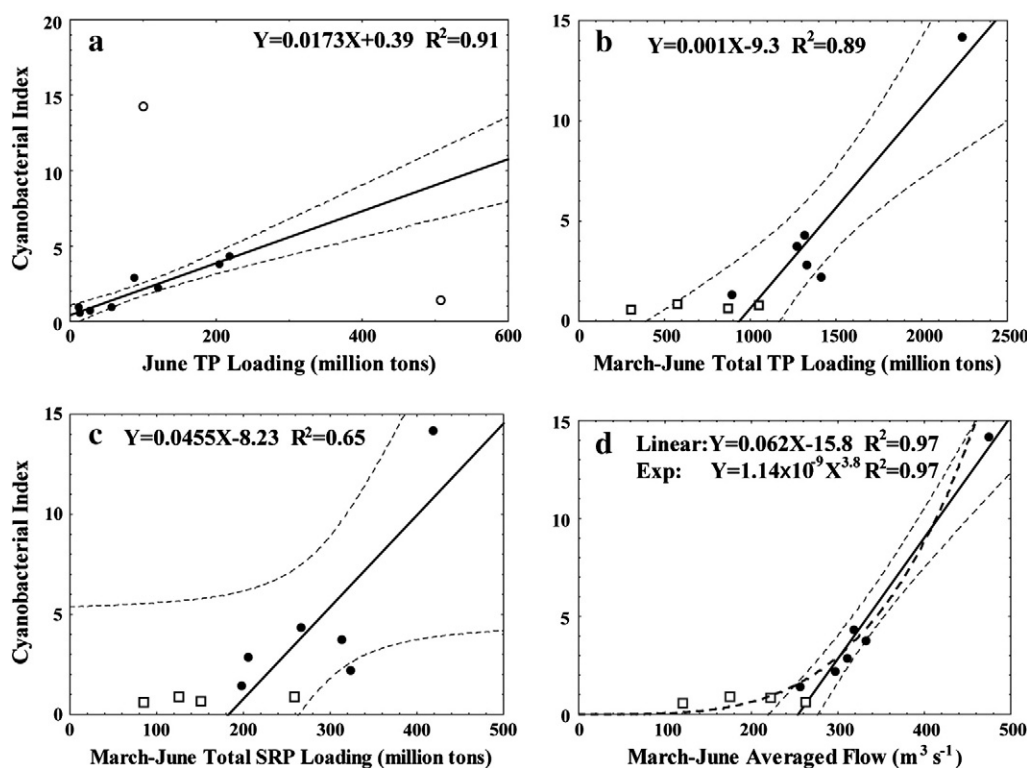


Fig. 3. The empirical relationships between cyanobacteria bloom intensity (Cyanobacterial Index) for western Lake Erie from 2002 to 2011 and phosphorus loads/river discharges of the Maumee River. (a) linear regression based on monthly TP loads for June for bloom years (closed circles), excluding 2004 and 2011 (open circles), RSE = 0.48; (b) linear regression based on cumulative TP for March to June for bloom years (closed circles), RSE = 1.75; (c) linear regression based on cumulative SRP for March to June for bloom years (closed circles), RSE = 3.1; and (d) linear (RSE = 0.96) and exponential (RSE = 0.58) regressions based on averaged river discharge for March to June for bloom years. The open squares represent the data for non-bloom years. Solid thick lines represent linear regression models and dashed thin lines indicate the 95% confidence intervals. Dashed thick line in (d) corresponds to the exponential regression model.

These figures are reproduced from Stumpf et al. (2012).

year data, which limits its applicability for projecting the cyanobacterial abundance in non-bloom years. Further, despite the suitability of these regression models for conducting rigorous predictive uncertainty analysis, Stumpf et al. (2012) did not include such an exercise in the original work. Another issue is that their verification will be dependent on the acquisition of new satellite imagery. This exercise will be more difficult until 2014 when the European Space Agency plans on launching a successor satellite to current MERIS. This new sensor would continue the capability demonstrated by MERIS into the future for further model development and validation. Overall, the results of Stumpf et al. (2012) emphasized the idea that spring nutrient loading can be a reasonable predictor of the cyanobacteria blooms in Lake Erie, and thus the corresponding river discharge and TP loading levels have the capacity to support seasonal forecasts.

Spatial and temporal trends in Lake Erie hypoxia, 1987–2007, by Zhou et al. (2013)

A novel geostatistical framework was recently presented by Zhou et al. (2013) to provide quantitative estimates of the hypoxia extent in the central basin of Lake Erie from 1987 to 2007. The Bayesian Information Criterion (BIC) was used to select the most parsimonious model, consisting of a subset of auxiliary variables (e.g., latitude, longitude, bathymetry, satellite-derived monthly-average sea surface temperature, and surface chlorophyll concentrations from April to September) that can reliably represent the spatial distribution of DO. Universal Kriging (UK) was then implemented to assess the dissolved oxygen spatial distribution using both the available DO observations and the auxiliary (explanatory) variables identified. Unlike the conventional regression though, the Universal Kriging model explicitly accounts for the spatial

correlation of the DO concentrations and operates as an exact interpolator in that all available observations are reproduced within their measurement error. An ad-hoc feature of the Zhou et al. (2013) model was the potential to generate realizations of processes conditional on observed quantities, which was effectively obtained through a “spatially-consistent” Monte Carlo approach aiming to provide equally-likely alternative DO distributions. These realizations followed the spatial covariance of all the available DO observations. Conditional realizations were generated for regions of the central basin with a depth greater than 15 m, and the hypoxic area was calculated for each realization by summing the areas with the DO concentrations below 2 mg L^{-1} . One thousand realizations were generated for each cruise, and the results were subsequently used to develop probabilistic estimates of hypoxic extent.

The time series of hypoxic extents were derived from the conditional realizations of the summer DO distribution from 1987 to 2007. Model results were qualitatively on par with other hypoxic extent reports in Lake Erie (Hawley et al., 2006; Makarewicz and Bertram, 1991). In particular, the model reproduced the decline of the hypoxic extent during the late 1980s to early 1990s as a result of the phosphorus load reduction programmes, as well as the subsequent increase due to the increase in non-point source phosphorus loading or the nutrient recycling mediated by dreissenid mussels. In regard to the robustness of the estimated hypoxic extents, it was found that months with larger hypoxic areas or cruises with fewer measurements were typically characterized by greater uncertainties. Namely, the uncertainties ranged from nearly zero when hypoxia was negligible (mid-September 2002), to nearly 6000 km^2 95% confidence intervals (e.g., September 1999) when the areas with estimated DO levels close to the 2 mg L^{-1} threshold are extensive, and thus can inflate the uncertainty of the exact hypoxia

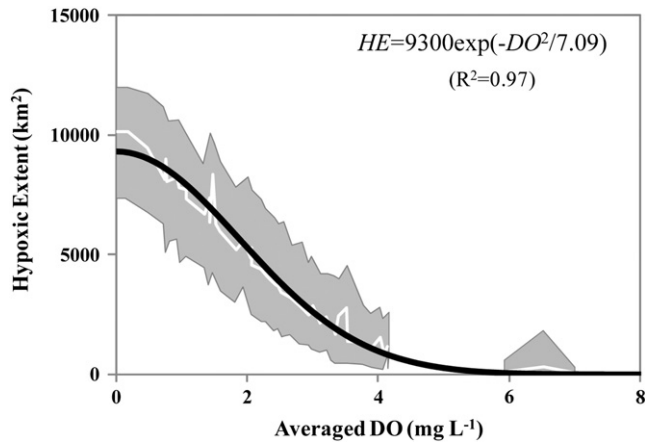


Fig. 4. The empirical model of hypoxic extent (*HE*) based on averaged DO from the ten index sampling stations in the central basin of Lake Erie. The thick black line represents the predicted *HE*. The observed mean value of *HE* is shown as a continuous white line and the grey areas are 95% confidence intervals. This figure is modified from Zhou et al. (2013).

magnitude. Further, Zhou et al. (2013) developed a simple exponential relationship for predicting hypoxic extent, using as predictor variable the average measured DO concentrations in ten regular sampling locations (Fig. 4). The latter exercise suggests that the ten regular sampling locations could be used as index stations for obtaining hypoxic extent estimates when detailed DO analyses are not done. The same study also highlighted the importance of considering the lake thermal structure (timing of stratification onset, hypolimnion thickness) in predictive frameworks that aim to elucidate the interannual variability of hypoxia in Lake Erie. Finally, unlike the previous models, this study does not provide any major insights into mechanistic linkages, but rather offered an important new dataset to which mechanistic models can be compared.

Discussion-future perspectives

In Lake Erie, a variety of statistical (data-driven) and mathematical (process-based) models have been developed to understand ecological interactions, to gain insights into the role of specific facets of the ecosystem functioning (internal loading, dreissenids), and to predict the response of the lake to external nutrient loading reductions. Generally, model-based environmental management is preferred to have stronger mechanistic foundation as this provides additional assurance that the models can reflect the functional changes in Lake Erie induced by significantly different external conditions. Nonetheless, developing a process-based model and invoking extra complexity raise critical questions in regard to the existence of commensurate knowledge of the multifaceted aspects of the system dynamics or even the capacity to depict them mathematically. Our review suggests that the evolution of their structural and functional complexity over the past 30 years significantly deviates from the proposed scheme in Fig. 2. Striving for the optimal balance between models that our prior knowledge tells us “much about little” or “little about much”, the local modelling efforts have mainly opted for the latter option, and thus they offered mainly heuristic tools to examine different ecological hypotheses and possibly dictate future data collection efforts. The majority of the recent process-based models are profoundly over-parameterized and have little capacity to support robust predictive statements. On a positive note though, the same modelling studies have rigorously quantified the goodness-of-fit or attempted to verify model performance in their extrapolation domain. What seems to be missing is a rigorous uncertainty assessment of the available models along with efforts to base the (much needed) ecological forecasts upon that uncertainty (Pappenberger and Beven, 2006).

As previously mentioned, the basic premise for the use of complex mechanistic models is to mimic the role of individual processes through proper mathematical description and realistic parameterization which can then collectively offer a faithful depiction of ecosystem dynamics. However, an important finding of our review is the considerable inconsistency with respect to the parameterization of the existing modelling constructs, e.g., the same biological rates can differ significantly among the different models. A characteristic example is the phytoplankton functional groups which have been characterized as having low ($<2 \text{ day}^{-1}$) or high (3 day^{-1}) maximum growth rates in Lake Erie, depending on the model considered (see the comparison of the Zhang et al. (2008) and Leon et al. (2011) models in Table 3). The maximum growth rate is an influential parameter that aims to characterize the average patterns of fairly diverse assemblages of phytoplankton species (Arhonditsis and Brett, 2005). The control of this maximum potential growth by the resource (temperature, light, and nutrient) limitations determines the growth rates realized during the phytoplankton simulations. Distinctly different phytoplankton characterizations can have profound implications in the predictive statements derived and may lead to significantly different projections when examining lake dynamics under alternative management scenarios (Gudimov et al., 2010; Ramin et al., 2011). We believe that this is a troubling practice that may stem from our tendency to treat the different parameters as numerical inputs for maximizing model fit, and not as surrogates of “real-world” processes that collectively aim to reproduce the ecosystem functioning. In the same context, it is also important to ensure that any new attempts to characterize the ecosystem functioning will not act as if they are “reinventing the wheel” (Mooij et al., 2010), but rather they should strive for a (reasonable) consistency with the existing modelling work in Lake Erie; unless there is evidence to challenge some of their founding assumptions.

It is also interesting to note that the reviewed eutrophication models have consistently used low half saturation constants for phosphorus uptake ($K_{\text{PO}_4} < 10 \mu\text{g P L}^{-1}$). Given the fairly low epilimnetic phosphate levels in Lake Erie, this specification downplays the likelihood of phosphorus limitation of the algal growth which deviates from recent empirical evidence from the system (Fitzpatrick et al., 2007; Moon and Carrick, 2007). If we also consider that both nutrient and light limitation have been included within the Liebig's Law of the Minimum, we believe that the role of light availability may have been overstated as the predominant factor of the bottom-up forcing in the system. Further, different mathematical expressions have been used to simulate key phytoplankton processes, such as the algal growth rates which have been modelled whether as a sole function of the ambient nutrient concentrations or as a two-pronged process that first considers the nutrient uptake rate in relation to the dissolved-phase nutrients and subsequently the growth rate as a function of their internal nutrient storage. Because the differences in the mechanistic foundation and parameterization of competing models can alter significantly the elicited predictive statements, we caution that the selection of mathematical equations and parameter values should not be based on subjective (and often arbitrary) criteria, but must be ecologically defensible and tightly linked to our contemporary understanding of the system. For example, someone may question the credibility of projecting the phytoplankton response to ambient nutrient variability without accounting for their intracellular storage capacity or properly considering the control exerted by herbivorous grazing in the current state of Lake Erie.

In the context of Lake Erie modelling, there is an increasing pressure to explicitly treat multiple biogeochemical cycles and to increase the functional diversity of biotic communities. In particular, all the recent modelling studies highlighted the inclusion of multiple nutrients along with the finer representation of phytoplankton communities, as necessary model augmentations for disentangling critical aspects of the lake dynamics, e.g., cyanobacteria dominance. Species populations are certainly more sensitive to external perturbations (nutrient enrichment, episodic meteorological events), and key biogeochemical processes

are more tightly linked to specific phytoplankton functional groups (Anderson, 2005). Nonetheless, the derivation of distinct functional groups from fairly heterogeneous algal assemblages poses challenging problems. Because of the still poorly understood ecology, we do not have robust group-specific parameterizations that can support predictions in a wide array of spatiotemporal domains. For example, preliminary efforts to incorporate phytoplankton functional types into biogeochemical models were based on speculative parameterization and – not surprisingly – resulted in unreliable predictions. Likewise, Zhao et al. (2008) showed that the reproduction of the typical seasonal succession phytoplankton patterns in freshwater ecosystems is quite fragile and only occurs within a fairly narrow window of the model parameter space. The latter study also pondered if it is “reasonable to expect single-valued data set-specific parameter estimates of artificially defined biotic entities to be extrapolated over a wide range of conditions?” A great deal of research is necessary to determine the optimal delineation of functional groups that demonstrate similar dynamics in certain environments, and to develop robust causal relationships that can be used in a broader range of conditions. There is little doubt that the capacity of the current generation of eutrophication models has not been proven yet, and therefore sceptical views in the modelling literature characterize all the efforts to simulate the dynamics of individual species or genera as attempts to “run before we can walk” (Anderson, 2005)! In this regard, we believe that the recent shift towards simpler causal models to link the nutrient loading variability with the occurrence of harmful algal blooms, and/or the hypoxia problems is certainly more prudent and will likely provide a solid foundation for guiding management decisions in the area (e.g., Stumpf et al., 2012; Zhou et al., 2013).

The effect of dreissenids on water quality is another critical aspect of the ecosystem functioning that requires robust modelling. Bierman et al. (2005) presented one of the most comprehensive models in the literature with respect to the ecology of dreissenids that builds upon earlier work by Schneider (1992). The model allows reproducing dreissenid filtration of particulate material from the water column, pseudofeces production, and excretion of dissolved-phase nutrients. The corresponding differential equation, however, calculates the rate of biomass change per individual in each age cohort class. Thus, if we aim to estimate the effects of the entire dreissenid mussel population at the ecosystem level, this model output needs to be multiplied by a “user-specified” and (in most cases) highly uncertain estimate of the number of individuals per age cohort class. Likewise, Kim et al. (2013) cautioned that none of the existing dreissenid submodels operates as a “real” population dynamics model, as they lack the ability to predict changes in spatiotemporal densities or their distributions among different age groups. On a similar note, the sediments represent another important controlling factor of the water quality in Lake Erie, acting as a source (or sink) for a wide variety of chemicals.

Closer to the sediment–water interface, intensive microbiological, geochemical, and physical processes determine the fraction of organic matter, nutrients, and pollutants released into the overlying water. Detailed knowledge of the processes occurring in the top few centimetres of the sediment is essential for the assessment of water quality, the understanding of the manifestation of hypoxia, and the management of surface waters. Diagenetic modelling is an indispensable tool to investigate the interplay among the sediment processes, to verify concepts, and to potentially predict system behaviours (Boudreau, 1997). This kind of diagenetic modelling as well as the data that necessitate to ground-truth those models (e.g., porewater analysis, phosphorus fractionation, organic matter profiles) is still missing in Lake Erie (Dittrich et al., 2013). Both field, experimental, and modelling work should be designed to shed light on the mechanisms of phosphorus mobilization in the sediments and to identify process controls under a variety of conditions. The knowledge obtained will allow addressing research questions, such as: Can phosphorus retention in lake sediments be predicted based on the sediment mineralogy, sedimentation substance

inputs, catchment type, and other characteristics? How sediment retention capacity with respect to phosphorus may respond to changes caused by human activities and/or climate change?

Another overlooked factor of the existing modelling work in Lake Erie is associated with the uncertainty underlying environmental models. Aside from the data used for their parameter specification, uncertainty can result from the model structure and input error (Beck, 1987). Model structure error is mainly associated with (i) the selection of the appropriate state variables for reproducing ecosystem behaviour, (ii) the selection of the suitable equations among a variety of mathematical formulations for describing the ecological processes, and (iii) the fact that our models are based on relationships which are derived individually in controlled laboratory environments but may not collectively yield an accurate picture of the real world dynamics. Recognizing the importance of the uncertainty problem, the recent model calibration practices tend to change from seeking a single “optimal” value for each model parameter, to seeking a distribution of parameter sets that all meet a pre-defined fitting criterion (Stow et al., 2007). These acceptable parameter sets may then provide the basis for estimating model prediction error associated with the model parameters. The importance of investigating the effects of uncertainty on mathematical model predictions has been extensively highlighted in the modelling literature, and there are a number of uncertainty analysis applications with simple or intermediate complexity models (Arhonditsis et al., 2007; Ramin et al., 2012). The three-dimensional constructs developed for Lake Erie are admittedly cumbersome for rigorous uncertainty analysis, but there are still ways to overcome this problem (e.g., linear or non-linear emulators) that have been profoundly overlooked by the local modelling community (Ratto et al., 2012). Some of the associated benefits, such as the expression of model outputs as probability distributions (Liu et al., 2011), the rigorous assessment of the expected consequences of different management actions (Arhonditsis et al., 2008), the optimization of the sampling design of monitoring programmes and the alignment with the policy practice of adaptive management (Zhang and Arhonditsis, 2008) will be particularly useful for stakeholders and policy makers when making decisions for sustainable environmental management in Lake Erie.

On a final note, the present evaluation of wide range of mathematical/statistical models implicitly pinpoints the uncertainty pertaining to the selection of the optimal model structure for a specific environmental management problem. However, we believe that the presence of various models with different strengths and weaknesses offers a unique opportunity for synthesis and improvement of the contemporary modelling practice in Lake Erie. Despite their simplicity, statistical models offer straightforward cause–effect relationships coupled with uncertainty estimates (e.g., response curves). Because they are founded upon the available data from the system, they offer a less risky choice to move forward and indeed offer a pragmatic means to obtain insight about the response of the system. Nevertheless, there are major limitations in their capacity to guide predictions outside the range associated with the dataset used. As an alternative, existing mechanistic models have significant heuristic value and potential to be used for predictive purposes, once rigorously evaluated. Recognizing that there is no true model of an ecological system, but rather several adequate descriptions of different conceptual basis and structure, model averaging is a means for obtaining weighted averages of the forecasts from multiple models of varying complexity (Ramin et al., 2012). Perhaps, one of the most promising ways to overcome the problem of structural uncertainty in aquatic ecosystem modelling may be to draw inference from this type of integrative statements. A number of methods exist to synthesize predictions across groups of models (ensembles), including sequential data assimilation approaches, such as the ensemble Kalman filter and ensemble particle filters (Moradkhani et al., 2006; Vrugt and Robinson, 2007) and post-hoc ensemble integration strategies, such as the Bayesian model averaging commonly used in weather forecasting (Raftery et al., 2005). In the context of ecological process-based modelling

though, this approach should not be viewed solely as a framework to improve our predictive devices, but rather as an opportunity to compare alternative ecological structures, to challenge existing ecosystem conceptualizations, and to integrate across different (and often conflicting) paradigms.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jglr.2014.02.014>.

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**A COMMENTARY ON THE MODELLING OF THE CAUSAL LINKAGES AMONG
NUTRIENT LOADING, HARMFUL ALGAL BLOOMS, AND HYPOXIA
PATTERNS IN LAKE ERIE**

(SUPPLEMENTARY MATERIAL)

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Figures Legends

Figure SI-1: Schematic diagram of the Lake Erie biogeochemical cycles for (a) oxygen; (b) nitrogen; (c) phosphorus; and (d) silica. Figures are reproduced from Di Toro and Connolly (1980).

Figure SI-2: Schematic diagram of the Lake Erie Dissolved Oxygen (DO) model (WCOD: Water column oxygen demand, SOD: sediment oxygen demand). Figures are reproduced from Rucinski et al. (2010).

Figure SI-3: Schematic diagram of the two-dimensional Lake Erie Ecological model. Figures are reproduced from Zhang et al. (2008).

Figure SI-4: Schematic diagram of the CAEDYM state variables in water column, benthos, and sediment. Figures are reproduced from Leon et al. (2011).

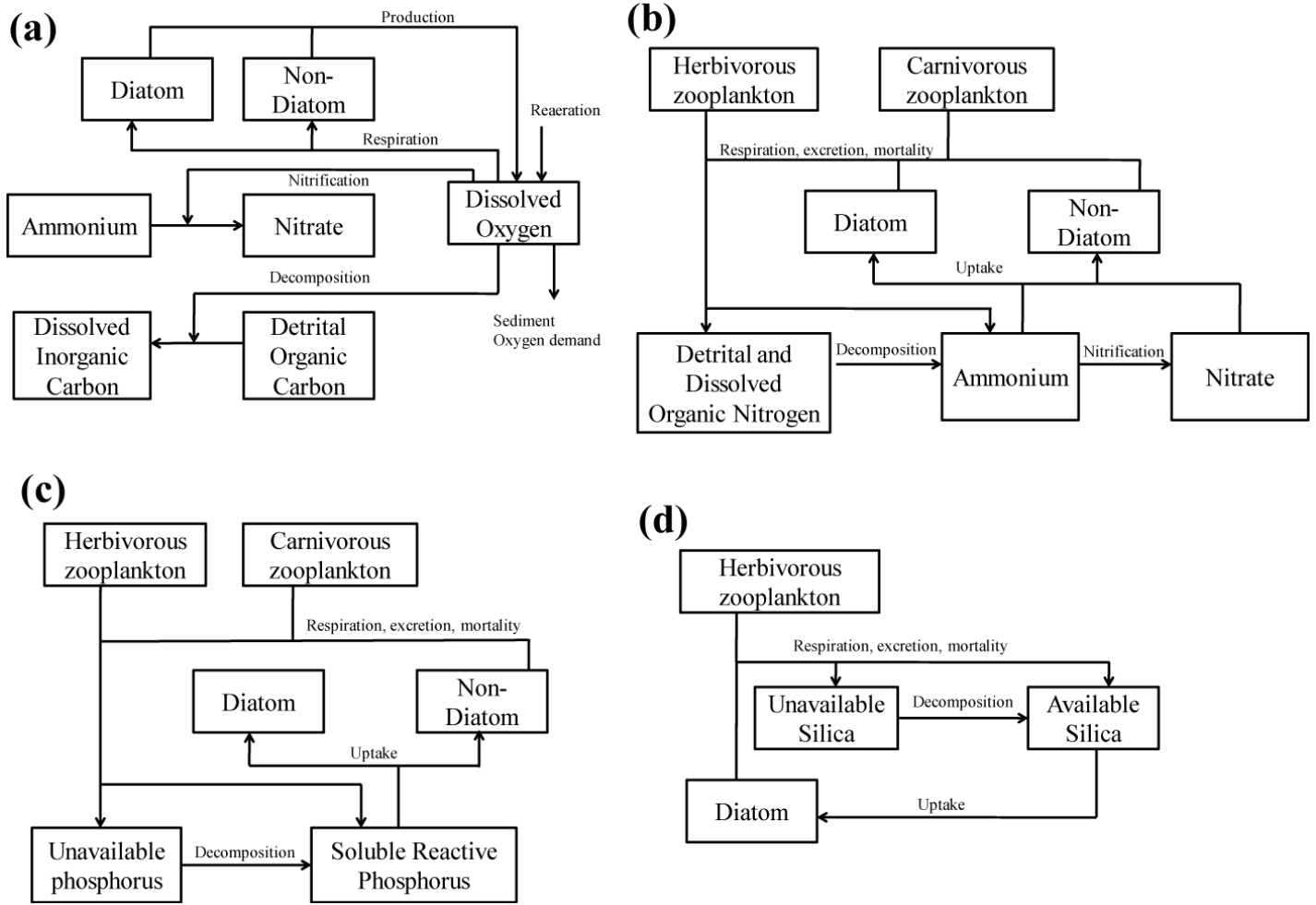


Figure SI- 1

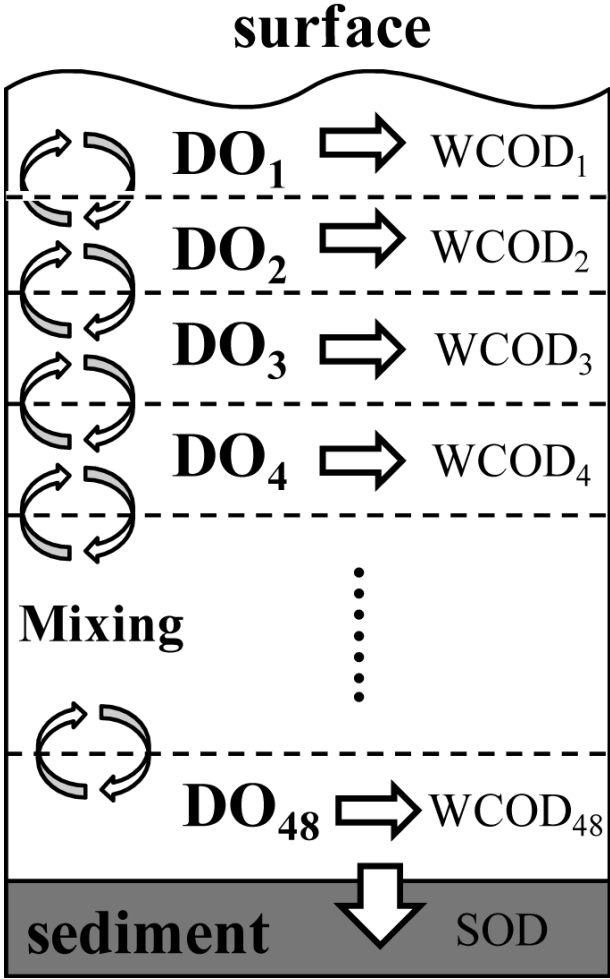


Figure SI- 2

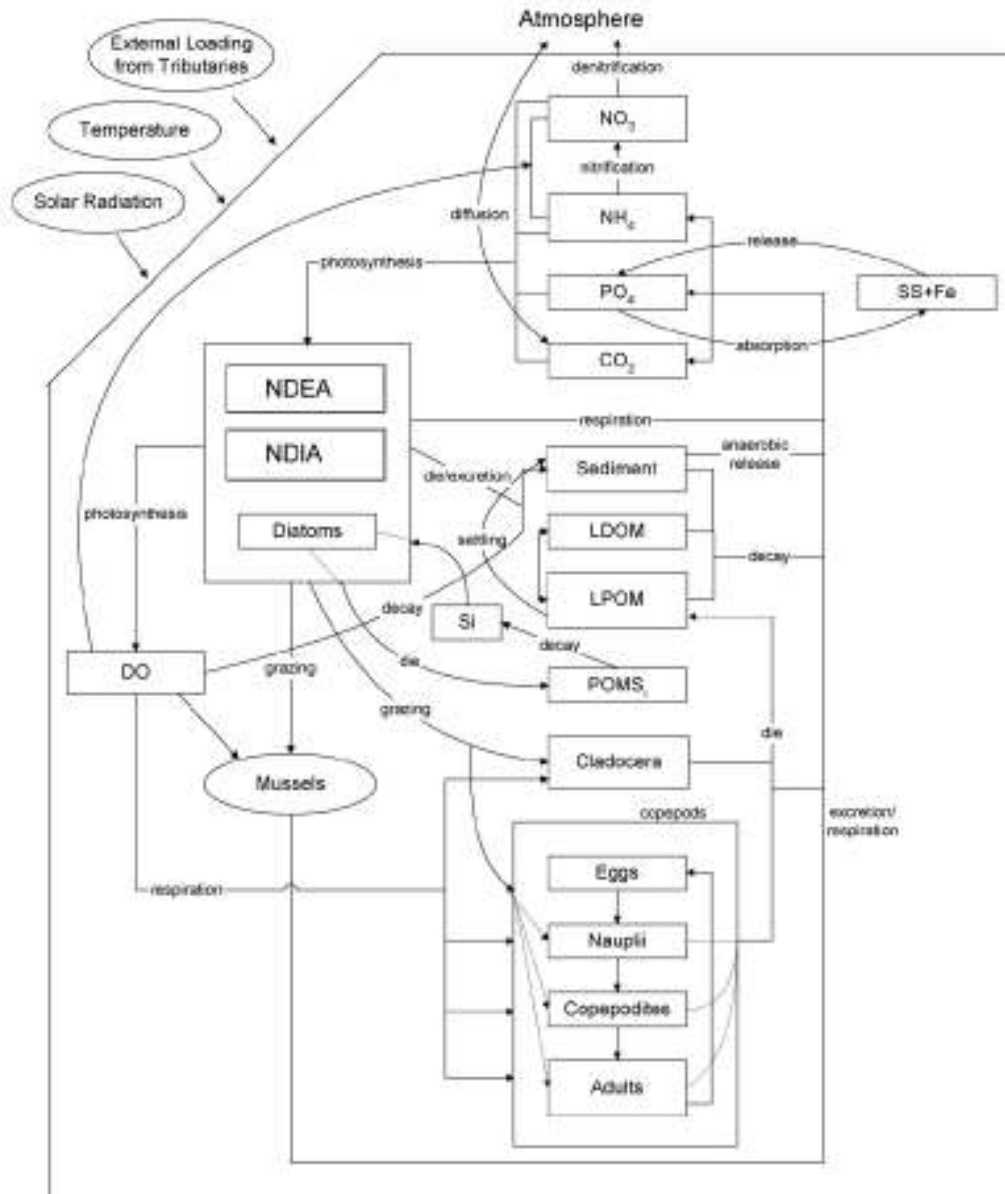


Figure SI- 3

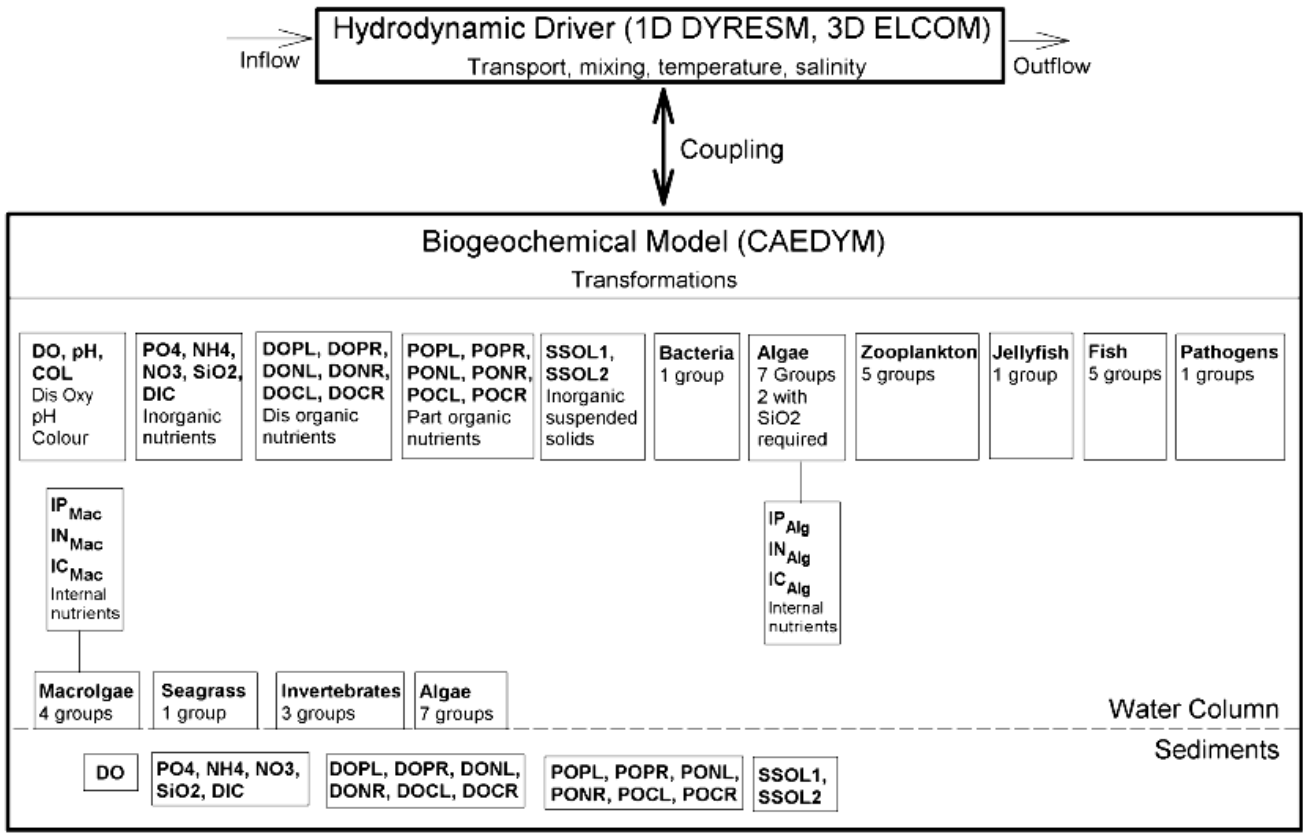


Figure SI- 4