Exploring, exploiting and evolving diversity of aquatic ecosystem models: a community perspective

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Abstract Here, we present a community perspective on how to explore, exploit and evolve the diversity in aquatic ecosystem models. These models play an important role in understanding the functioning of aquatic ecosystems, filling in observation gaps and developing effective strategies for water quality management. In this spirit, numerous models have been developed since the 1970s. We set off to explore model diversity by making an inventory among 42 aquatic ecosystem modellers, by categorizing the resulting set of models and by analysing them for diversity. We then focus on how to exploit model diversity by comparing and combining different aspects of existing models. Finally, we discuss how model diversity came about in the past and could evolve in the future. Throughout our study, we use

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analogies from biodiversity research to analyse and interpret model diversity. We recommend to make models publicly available through open-source policies, to standardize documentation and technical implementation of models, and to compare models through ensemble modelling and interdisciplinary approaches. We end with our perspective on how the field of aquatic ecosystem modelling might develop in the next 5–10 years. To strive for clarity and to improve readability for non-modellers, we include a glossary.

Keywords Water quality · Ecology · Geochemistry · Hydrology · Hydraulics · Hydrodynamics · Physical environment · Socio-economics · Model availability · Standardization · Linking

Introduction

The societal niche for aquatic ecosystem models: developing short-term and long-term management strategies

Aquatic ecosystems provide a range of ecosystem services (Finlayson et al. 2005), in particular by being sources and sinks for natural resources and anthropogenic substances. For example, as a source, they provide water for drinking, irrigation, hydropower and industrial processes. Moreover, they provide many food products. More recently, their aesthetic and recreational value has been recognized with associated health benefits. Aquatic ecosystems also act as a sink for various substances, including sewage, agricultural run-off, discharge from impoundments, industrial waste and thermally polluted water. Equally important, they provide a critical habitat for organisms that form an important part of the biodiversity. Each of the anthropogenic and natural source functions puts specific requirements on the quality of the aquatic ecosystem (Postel and Richter 2003; Keeler et al. 2012). At the same time, these quality requirements can be hampered by both the source (through overexploitation) and the sink (through pollution) functions of the aquatic ecosystem. Aquatic ecosystem models (hereafter referred to as AEMs) frequently play a role in quantifying ecosystem services and developing strategies for water quality management (Jørgensen 2010; Mooij et al. 2010). The AEMs used for this purpose are often engineering-oriented based on accepted theory and methodology for routine applications. Engineering models may be complex and linked to one another, but components are always tested. Using projections and scenario
analyses, engineering-oriented AEMs can assess the various source and sink functions to help optimize and understand aquatic ecosystem function in terms of human and conservation needs. For example, AEMs have been applied as management tools to evaluate the efficiency of eutrophication mitigation strategies, to understand oceanic dynamics (e.g., the global carbon cycle), and to predict biotic responses to climate change (Arhonditsis and Brett 2004). AEMs can also be used for near real-time modelling and forecasting to facilitate immediate management decisions on, for instance, the shutdown of drinking water intakes (Huang et al. 2012; Silva et al. 2014) or the suitability of water for swimming (Ibelings et al. 2003).

The scientific niche for AEMs: advancement of theory

A strong scientific motivation for the development of AEMs is to encapsulate and improve our understanding of aquatic ecosystems. For instance, scientific AEMs can help to close mass balances of essential elements such as carbon, nitrogen and phosphorus and thereby allow quantifying the role of aquatic systems in national and global carbon and nutrient budgets (Robson et al. 2008; Harrison et al. 2012). Keeping track of mass balances can also provide help in answering stoichiometric questions (Giordani et al. 2008; Li et al. 2014). Additionally, scientific AEMs can help untangle the feedbacks between aquatic biodiversity and aquatic ecosystem functioning (Bruggeman and Kooijman 2007), and also achieve an integrated ecosystem health assessment (Xu et al. 2001). Yet another timely research topic studied with models is assessing the resilience of ecosystems to changes in external forcing arising from nonlinear functional relationships between ecosystem components (Ludwig et al. 1997; Scheffer et al. 2001). This has been done by analysing the strength of various positive and negative feedback loops in the socio-ecological system (Van Der Heide et al. 2007; Downing et al. 2014). Such studies generate new hypotheses that can then be tested in laboratories or in the field. Models are therefore effective scientific tools because they allow undertaking ‘virtual experiments’ that would be too expensive or impractical to carry out in real-world systems (Meyer et al. 2009).

The methodological niche for AEMs: filling data gaps and inverse modelling

Another motivation to develop AEMs is to fill gaps in observations. For instance, some quantities (e.g., primary production) are measured at high spatial
resolution, but at a low temporal resolution and vice versa. Modelling then allows for interpolation in space and time such as seen in climatology (Jeffrey et al. 2001). Other examples include interpolating through time between satellite images or across space to fill gaps caused by cloud cover (Hossain et al. 2015). Inverse modelling is another application within the methodological niche for AEMs, in which specific system parameters or process rates that are difficult to measure are estimated. In contrast to forward modelling, inverse modelling uses observations to estimate the processes or factors that created these observations (Tarantola 2005). Since inverse modelling in general lacks a unique solution, it is important to include all a priori information on model parameters and processes to reduce the uncertainty on the results (Tarantola 2005; Jacob 2007). Methods used for inverse modelling include Bayesian inference, often used with the Markov chain Monte Carlo technique (Press 2012; Gelman et al. 2014) and Frequentist inference (Press 2012). Different software packages for implementation of these methods exist (Vézina and Platt 1988; Reichert 1994; Lunn et al. 2000; Soetaert and Petzoldt 2010; Van Oevelen et al. 2010; Doherty 2015).

Existing diversity in AEMs

Due to numerous potential AEM applications (in an analogy to biodiversity, we refer to these as ‘model niches’), scientists began to develop these models in the 1960s, in tact with the availability of the necessary computing infrastructure to implement them (e.g. King and Paulik 1967). Since then, an array of AEMs has been developed around the world, with each development directed by a specific set of questions and hypotheses. In many cases, investigators and engineers implemented their own models rather than starting with an existing model. While this practice of creating one’s ‘own model’ can be criticized because it bears the inefficiency of ‘reinventing the wheel’ (Mooij et al. 2010), it has produced a great diversity in approaches, formulations, complexity and applications, which can be seen as an advantage. In addition, the extra investment is often compensated by a more efficient model application for the issue at hand and a better model understanding. Furthermore, the availability of modelling resources through the Internet provides new opportunities to explore and exploit this diversity and will most likely affect the evolution of model diversity in the near future.

A working definition of what constitutes an AEM

This paper aims to present a current perspective on how we can explore, exploit and evolve the existing diversity in AEMs as seen by a diverse and international community of aquatic scientists (the authors). We try to reach out to not only the skilled modellers, but also aquatic ecologists who are inexperienced in modelling. To make this study feasible, we need a definition of what constitutes an AEM. Here, we define an AEM as ‘a formal procedure by which the impact of external or internal forcing on aquatic ecosystem state(s) can be estimated’. In most cases, AEMs cover many processes and are spatially explicit, but both are not a prerequisite. According to our definition, a minimal model that qualitatively describes the ecosystem response to external forcing also qualifies as an AEM (Fig. 1). We exclude models that focus on one single component of an ecosystem (e.g. models that only deal with the population dynamics of a given species), but include models that zoom in on one part of the ecosystem (e.g. the fish or macrophyte community) while treating the remainder of the ecosystem in an aggregated way (typically through the use of carrying capacities or mortality rates). Two distinct classes of AEMs exist: those that formulate a direct mathematical relation between forcing and state (statistical models), and those that are formulated in terms of the processes underlying this relation (process-based models). Statistical models directly link forcing and state that can be derived from data with standard statistical techniques. Linking process-based models to data involves less
standardized calibration and validation techniques. The advantage of process-based models is that they provide insight into the mechanisms underlying change and recovery. This study is primarily focussed on the diversity in process-based models, although we acknowledge the diversity and usefulness of statistical models that directly link forcing and state. AEMs, as defined here, combine elements from a number of scientific modelling disciplines (Fig. 2). In addition to defining what constitutes an AEM, we developed a glossary of terminology used in the field of aquatic ecosystem modelling (given in Text Box 1). The purpose of this glossary was to strive for clarity within the context of this study. This glossary may also be of help to newcomers in the modelling field. While working on the glossary, we noted that it is impossible to make a clear distinction between models (the mathematical description of a system), their implementation (e.g. software packages) and their applications (where model inputs/parameters are adapted to a specific ecosystem and confronted with data) because there is great diversity in how these components are perceived and combined by different modellers.

How this study is structured

We first focus on exploring AEM diversity by discussing approaches to inventorize, categorize and document these models and finally present a more formal analysis of model diversity. To support our discussion, we compare a number of AEMs, hydrological and hydrodynamic drivers, relevant modelling approaches and supportive software for model implementation and model analyses that came about in a survey among modellers participating the third AEMON (Aquatic Ecosystem MOdelling Network) workshop held in February 2015. To put our analysis in perspective, we compare the number of AEMs, hydrological and hydrodynamic drivers, relevant modelling approaches and supportive software for model implementation and model analyses with published lists (Table 1). We cover both marine and freshwater AEMs, with a bias towards the latter group. All data can be found in Online Resource 1. It is remarkable that earlier attempts by Benz et al. (2001) have little overlap with our overview, which shows that there is a greater diversity than presented here. We then focus on exploiting diversity and ask several questions. How can we make use of the full breadth of expertise captured in existing AEMs, and how can we easily switch between spatial configurations or software packages to run and analyse the models using package-specific tools? We continue with stressing the
potential of ensemble modelling, and we end this section with a discussion on how to exploit the full range of approaches used in aquatic ecosystem modelling. In the section on evolving diversity, we describe the origins of the current diversity in AEMs and discuss how model diversity could evolve in the future and how standardization can facilitate this process. In the final section, we discuss how we can learn from concepts and techniques in biodiversity research in our study on model diversity. Finally, we provide a list of practical recommendations and a perspective for the field of aquatic ecosystem modelling in the next decade.

Exploring diversity in AEMs

AEMs have been and are being developed independently in many places around the world. In this section, we explore model diversity.

Making an inventory of the diversity in AEMs

An exploratory survey among 42 modellers participating in the third AEMON workshop 2015 resulted in 133 different models, packages or programming languages in use in the field of aquatic ecosystem modelling (data presented in Online Resource 1, Datasheet 2). We performed a Redundancy Analysis (RDA, using the methods of Oksanen et al. 2014) on 39 AEMs from this list (results in Online Resource 2). This analysis demonstrates that the professional affiliation and country of origin played an important role in determining knowledge and usage of models. The driver behind this could be the research group’s background, but also the diverging needs that motivated the development of models, such as whether there are mainly shallow lakes or deep reservoirs in a specific country. Three approaches seem suited for developing a more formal and ongoing inventory of model diversity: (1) lists, (2) wikis and (3) code repositories. We are not aware of an up-to-date list of AEMs with a good coverage of the field. Laudable attempts to list ecological models are UFIS (Knorrenschild et al. 1996) and the ECOBAS initiative by Joachim Benz (http://www.ecobas.org, Benz et al. 2001). ECOBAS provides metadata on a wide range of models, including hydrological, hydrodynamic, meteorological and ecological models. However, the website has only rarely been updated since 2009;
updating is a challenge for any top-down initiatives. An alternative could be an open community-based approach, such as wikis, where multiple editors independently contribute information. The obvious and overwhelmingly successful example of this approach is Wikipedia (http://www.wikipedia.org) which maintains many lists, for instance of programming languages (http://en.wikipedia.org/wiki/List_of_programming_languages). The potential lack of consistency of such community-based lists seems to be compensated by the scope and immediacy of the information provided and the commitment resulting from the community-based approach. The third option is code repositories, such as SourceForge (http://sf.net) and GitHub (http://github.com), which are increasingly popular platforms enabling open-source communities to develop software and distribute code.

Documenting diversity in AEMs

To preserve and communicate model diversity, proper documentation of models is crucial. There is no standard way of documenting AEMs, and different model developers have different methods to obtain and save their information. The existing ODD protocol (overview, design concepts and details) for individual-based models (Grimm et al. 2006), the Earth System documentation project (http://es-doc.org) or the TRACE approach (TRAnsparent and Comprehensive Ecological modelling documentation) might be adopted by aquatic ecosystem modellers in the future (Grimm et al. 2014). Models can be documented through model homepages, scientific publications or grey literature reports. Wikipedia is not an option because it has a strict policy of not being a primary source of documentation but instead only providing referenced information. To be useful in the current practice of scientific research, any type of documentation should be accessible through the Internet, preferably with open access. The majority (71 %) of the AEMs analysed in Online Resource 3 has a website that provides model documentation. Furthermore, for 86 % of the models, we could identify a primary publication; however, only three out of 42 AEMs analysed in Online Resource 3 have a page on Wikipedia (Ecopath, PCLake and PCDitch).

Categorizing diversity in AEMs

To cope with the diversity in models, some form of categorization is useful. ‘Bining’ models in clearly defined categories provide an overview for newcomers and experts, and help to identify what is missing. From the list of models in Online Resource 1, Datasheet 2, we selected those models that can be classified as an AEM according to our definition. This resulted in a list of 42 AEMs (see for data Online Resource 1, Datasheet 3). For these models, we were able to obtain metadata from experts to categorize them (see Online Resource 3 for all the details and see Text Box 1 for an explanation of all the technical terms used below). For the modelling approach, it was found that over 75 % of the models were qualified as being dynamic, process-based, biogeochemical, mass-balanced, compartmental or complex dynamical (Fig. 3a). Over 45 % of them were qualified as being stoichiometric or spatially explicit as well as being a competition, a consumer-resource, a food web or a community model. About 25 % of them were qualified as being of the NPZD type of model (nutrients, phytoplankton, zooplankton, detritus) as well as being a hydrodynamic model. One out of seven of these models contained individual-based approaches, more specifically being an individual-based community model, a trait-based model or a dynamic energy budget model. The 42 AEMs cover every aquatic habitat, with 22 % of models claiming global applicability (Fig. 3b). Eutrophication is an application domain of no less than 98 % of the analysed models (Fig. 3c). Next, in decreasing order of importance are climate change, carbon cycle, fisheries, biodiversity loss and adaptive processes. 90 % of the 42 models allow for dynamic simulations (Fig. 3e). The remaining models are based on statistical relations. About half of the models are implemented in frameworks that have tools for sensitivity analysis, calibration, validation and uncertainty analysis. Here, we define a framework as a software package that can be combined with user-written code to create a software application (for a more extensive definition, see Text Box 1). Tools for bifurcation analysis are less common. Over two-third of the models are implemented within an existing modelling framework, with the R/deSolve package (Soetaert et al. 2010) and the Framework for Aquatic Biogeochemical Models.
(FABM) (Bruggeman and Bolding 2014) being the most used of the 12 modelling frameworks that we encountered (Fig. 3d). One can rightfully say that the field of aquatic ecosystem modelling is quite scattered when it comes to the use of modelling frameworks. This notion was one of the incentives for developing Delft3D-Delwaq (Deltares 2014), FABM (Bruggeman and Bolding 2014) and the Database Approach to Modelling (DATM) (Mooij et al. 2014). With 50%, FORTRAN is the dominant programming language for coding AEMs (Fig. 3f). Next comes C or C++ (together 26%), Delphi (15%) and R (15%). The majority of AEMs are implemented as ordinary or partial differential equations (Fig. 3g).
Analysing diversity in AEMs

Analysing model diversity goes beyond the more descriptive approach mentioned above. Here, the aim was to identify whether we are dealing with true diversity or ‘pseudo-diversity’. Models are often related to each other. The MyLake model (Saloranta and Andersen 2007), for example, has characteristics that are also found in other lake models such as DYRESM-CAEDYM (Hamilton and Schladow 1997), MINLAKE (Riley and Stefan 1988), PROBE (Blenckner et al. 2002) and BELAMO (Omlin et al. 2001; Mieleitner and Reichert 2006). We aim for a more objective and in-depth analysis of a list of AEMs using a similarity index (for details on the analysis, see Online Resource 4 and for the data Online Resource 1, Datasheet 4). One approach is to compare state variables between models. We analysed 24 AEMs for which sufficient information was provided, which gave in total almost 550 unique state variables. The minimum number of state variables found in a model is 2 and the maximum is 118 (Fig. 4). It should be noted that in some (especially the larger and general) models, not all state variables are included simultaneously in each model application but rather subsets of variables are being used. Additionally, some models have state variables that can be duplicated by changing their parameters (e.g. cohorts of a species). A Sørensen similarity analysis (Sørensen 1948) using the state variables of 24 models (Online Resource 4) shows that models become more similar as their complexity increases. This is an expected result as the chance of similarities increases with increasing sampling size of a given pool. However, overall the dissimilarity is higher than the similarity since more than 80 % of the models have a similarity index of less than 0.25. Hence, many models benefit from predecessor models even though they are still unique with individual features not found in predecessor models. Most overlap can be found in general state variables such as phosphorus, ammonia and a generic group of phytoplankton or zooplankton. Three groups of models can be distinguished: general-purpose models with a relative high overlap, specialized models with low overlap and intermediate models with an intermediate level of overlap (see dendrograms in Online Resource 4). Interestingly, some models are significantly more dissimilar than would be statistically expected based on their number of state variables (red downward arrow, Fig. 4). This is because these models capture only a specific non-overlapping part of the aquatic ecosystem (e.g. the Guam Atlantis Coral Reef Ecosystem Model versus PCLake or CAEDYM). Other models are more similar than would be expected based on the number of state variables (upward green arrow); these models simulate the aquatic ecosystem in a more general way, such as CCHE and Mylake. A following step could be to compare the models for their mathematical process formulations, though this is beyond the scope of this paper. An educated guess is that this will reveal an even higher diversity, as endless combinations can be made with the available process formulations. For example, Tian (2006) counted 13 functions used to describe the effect of light forcing on phytoplankton growth. Using these light functions in combination with other functional relations, for instance, temperature forcing (10 different relations), zooplankton feeding (20 different relations), prey feeding (15 different relations) and mortality (8 different relations), lead to hundreds of thousands of combinations that give different results and are all ‘the best’, depending on the aim of the model (Gao et al. 2000).

Exploiting diversity in AEMs

The inventory of the AEMs reveals a great diversity in model approaches, formulations and applications. Here, we ask whether and how this diversity could be exploited.

Exploiting the diversity in disciplines

One of the options is to exploit the diversity in contributing disciplines (see Fig. 2) and work in teams consisting of not only aquatic ecologists, but also social scientists, economists, climatologists, hydrologists, statisticians, mathematicians, etc. Working in an interdisciplinary setting helps one to look beyond the personal expert field and provides a more holistic view upon both models and aquatic ecosystems (Hamilton et al. 2015). Resulting interdisciplinary models have an increased complexity with the disadvantage that full understanding of the model by the individual modeller is lost (Scholten et al. 2007; Robson 2014a). The problem of inappropriate usage of complex models can be overcome by again working in
interdisciplinary teams. In this way, team members are able to focus on their own area of expertise while the team as a whole is able to understand the full model. Statisticians and mathematicians can support interdisciplinary teams with their knowledge on mathematical formulations and their insight into model uncertainty. Especially within the scientific niche, understanding of the model is important since novel ideas need to be tested and understood. Within the engineering niche, there is less need to understand each model component in detail. Indeed, many people drive a car safely without having a detailed technical background on the engine’s functionality.

Exploiting the diversity in spatial explicitness of AEMs

Another way to exploit the diversity in AEMs is by using the full width of spatial explicitness, which varies from spatially homogenous (0D) and vertically
or horizontally structured (1D) to fully 3D. Within these dimensions, a modeller can additionally choose between different structured grids (e.g. Cartesian grid, regular grid and curvilinear grid) and unstructured grids (e.g. finite elements). Following Occam’s razor, model complexity should be minimized and only increased if this increases the predictive performance of the model or its generality/universality (please note that, while mentioned here in the context of spatial explicitness, Occam’s razor applies to all aspects of complexity in AEMs). Therefore, to understand the basics of ecological processes in a well-mixed system, one should use a 0D model as its dynamics are often easier to understand. Additionally, 0D models are well suited for checking the internal consistency of the model functions. Spatially explicit models, however, are more realistic, as they account for the spatial heterogeneity of ecosystems, with the risk of getting lost in complexity when explaining model behaviour. Nonetheless, some research questions cannot be solved without taking spatial resolution into account [e.g. population dynamics of fish in Jackson et al. (2001), and spatial distribution of macrophytes and algae in Janssen et al. (2014)]. Recent advances facilitate the implementation of a model in different spatial settings. For example, with Delft3D-Delwaq, FABM and DATM, it is possible to switch between a 0D, 1D, 2D to 3D implementation of, for instance, PCLake (Van Gerven et al. 2015). However, these frameworks are currently implemented without accounting for feedbacks between ecology and hydrodynamics. Interfaces such as OpenMI (Gregersen et al. 2007) and FABM (Bruggeman and Bolding 2014) allow for such coupling and are designed to overcome the issues that emerge when integrating ecology and hydrodynamics. Examples of these issues are the different timescales and spatial schematization for ecology and hydrodynamics (e.g. Sachse et al. 2014) and feedbacks between ecology and hydrodynamics, such as the effects of water plants on the water flow (e.g. Berger and Wells 2008).

Exploiting diversity by having a given AEM implemented in multiple frameworks

Recent approaches such as DATM (Mooij et al. 2014), FABM (Bruggeman and Bolding 2014) and the open process library in Delft3D-Delwaq (Deltasres 2014) make it possible to exploit model implementations in multiple frameworks without much overhead. Therefore, a myriad of tools for model analysis (e.g. sensitivity analysis, calibration, validation, uncertainty analysis, and bifurcation analysis) become easily available. The redundancy in tools among frameworks insists modellers to stick to the framework they are familiar with for most analyses, whereas the complementarity in tools is tempting to switch to other frameworks for alternative analyses (Van Gerven et al. 2015), including the switch between 0D and 3D. In this way, the strengths of frameworks (including runtime) can be exploited, and the underlying ecological question can be approached from different perspectives.

Exploiting diversity in dealing with uncertainty in AEMs

As a simplification of nature, AEMs suffer from uncertainty in their outcomes (Beck 1987; Chatfield 1995; Draper 1995). Sources of uncertainty are structural uncertainties, i.e. incomplete or imperfect process formulations, parameter uncertainty, uncertainty in forcing functions and initial values, uncertainty in validation data, and uncertainty due to the numerical methods used. A full coverage of the topic of uncertainty in AEMs is beyond the scope of this paper. For more information on this topic, we refer to the extensive literature available on this topic including Beck (1987), Chatfield (2006) and Doherty (2015). Below, we limit ourselves to presenting three different views on how to deal with uncertainty in parameters. First, a modeller measures the parameters’ magnitudes directly. The parameter values are then purely based on biologically, chemically or physically knowledge. Due to errors in the measurements (experimental uncertainty, Moffat 1988) and limited transferability (e.g. between laboratory and field conditions), these a priori parameter values have an uncertainty as well (Draper 1995). By repeating the measurements over and over, the experimental uncertainty can be reduced, thereby minimizing the parameter uncertainty, but this is often a costly measure (Chatfield 1995). A second option is to estimate the parameters using calibration data and statistics without the use of a priori knowledge. This method leads in many cases to multiple possible parameterizations of the model with equal fit
(e.g. Beven 2006) and bears the risk of overfitting (Hawkins 2004). For this reason, a modeller may choose for the third option where the parameters are estimated based on calibration data, statistics and priori knowledge (e.g. Janse et al. 2010). In this case, a realistic range of parameter values is defined, prior to the parameter estimation by statistics. Thereafter, using Bayesian statistics, the parameters can be estimated within the range of realism (Gelman et al. 2014).

Exploiting diversity by ensemble modelling with AEMs

One way to deal with the uncertainty is using the diversity of models in ensemble techniques [e.g. Ramin et al. (2012) or Trolle et al. (2014), see Fig. 5 for an example from the latter study]. A variety of ensemble techniques exists, each duplicating a certain aspect of the modelling process. In multi-model ensembles (MMEs), multiple models are applied to a given problem. Single-model ensembles use different model inputs (parameters, initial values, boundary conditions) to exploit the model’s sensitivity (e.g. Couture et al. 2014; Gal et al. 2014 or Nielsen et al. 2014). More ensemble techniques or combinations of techniques exist including multi-scheme ensembling (use of different numerical schemes) and hyper-ensembling (use of multiple physical processes). Ensemble modelling has become a standard in meteorological forecasting (e.g. Molteni et al. 1996) and climatic forecasting (e.g. IPCC 2014). There is an increasing number of applications in hydrology and hydrodynamics as well (e.g. Stepanenko et al. 2014; Thiery et al. 2014). In aquatic ecosystem modelling, the use of ensemble techniques is still rare (but see examples in, for instance, Lenhart et al. 2010; Ramin et al. 2012; Gal et al. 2014; Nielsen et al. 2014; Trolle et al. 2014). However, the relevance of MME for ecological modelling is large, as a strictly physically based description is not practically feasible and a unified, transferable set of equations is, therefore, not available. Additionally, we foresee that ensemble modelling will become common practice because of (1) the emergence of active communities of aquatic ecosystem modellers such as AEMON; (2) the increase in freely available papers, data and model code; and (3) the development of approaches such as Delft3D-Delwaq, FABM and DATM. Hence, the results of decades of individual model niche development can now be better utilized (Mooij et al. 2010; Trolle et al. 2012). The comparative list provided in Online Resource 1 (Datasheet 4) is a useful starting point of ensemble modelling with AEMs. When using a model to provide forecasts, MME have two major advantages over single-model approaches. First, the ensemble mean may be a better predictor than any of the sole ensemble members (Trolle et al. 2014). This is especially true when an aggregated performance measure over many diagnostics variables is considered.

![Fig. 5 Example of a multi-model ensemble (MME). The shaded area shows the full width of predicting outcomes made by different models, the black line shows the mean of all models and the circles are the observations. Figure modified after Trolle et al. (2014) where the authors show that the prediction by the average model outcome is better than the prediction by individual models](image-url)
Second, the ensemble spread can serve as a convenient measure of predictive uncertainty if a spread–skill correlation exists. Although MMEs are attractive, their limitations need to be recognized. First, despite ever increasing computer power, they are time-consuming to put in place. More importantly, MME-based estimates of structural uncertainty can only be meaningful if the models involved differ substantially. Another more general limitation of ensembles is that the attainable estimate of uncertainty is inevitably incomplete, for example due to a limited number of suitable models and the requirement of each model to have its own set of—ideally standardized—parameters and initial values. Ensemble techniques therefore only quantify part of the total uncertainty in predictions (Krzysztofowicz 1999). In the context of ecological process-based modelling though, the integration of multiple models should not be viewed solely as an approach to improve our predictive devices, but also as an opportunity to compare alternative ecological structures, to challenge existing ecosystem conceptualizations, and to integrate across different (and often conflicting) paradigms (Ramin et al. 2012). Future research should also focus on the refinement of the weighting schemes and other performance standards to impartially synthesize the predictions of different models. Several interesting statistical post-processing methods presented in the field of ensemble weather forecasting will greatly benefit our attempts to develop weighting schemes suitable for the synthesis of multiple ecosystem models (Wilks 2002). Other outstanding challenges involve the development of ground rules for the features of the calibration and validation domain, the inclusion of penalties for model complexity that will allow building forecasts upon parsimonious models, and performance assessment that does not exclusively consider model endpoints but also examines the plausibility of the underlying ecosystem structures, i.e. biological rates, ecological processes or derived quantities (Arhonditsis and Brett 2004).

Exploiting the diversity in fundamentally different approaches in aquatic ecosystem modelling

Finally, we could exploit the diversity in more fundamentally different model approaches, for example statistical- versus process-based models. The diversity in model approaches is the product of the numerous choices that can be made during model development, pursuing a certain trade-off between effort, model simplicity, realism, process details, boundary conditions, forcings and accuracy along various dimensions such as time and space (e.g. Weijerman et al. 2015). For example, minimal models aim to understand the response curve of ecosystems to disturbances, but they are generally too simple to allow for upscaling and process quantification. Complex models on the other hand can describe the cycling of nutrients through many compartments of an ecosystem as well as the flow of energy through the system. Therefore, they often allow for quantitative scenario evaluations, but their output is difficult to interpret as it is demanding to decipher the numerous interactions and feedback loops. More complexity also can be introduced by individual-based and trait-based models, which allow the inclusion of evolutionary processes. Thus, a higher diversity of model approaches permits addressing a higher number of different purposes, provided that they are sufficiently complementary. There is a great value in combining different modelling approaches, as insights gained by one model can be useful for the application of another, and we benefit from the strengths of different model types (Mooij et al. 2009). Combining modelling approaches helps to develop an integrative view on the functioning of aquatic systems and seems almost essential for the adaptive management of the source and sink functions of lake ecosystems, which require integrated thinking and decision support.

Evolving diversity in AEMs

We have explored and exploited diversity in AEMs. Before reflecting on possible future evolution of model diversity, it is interesting first to look back and see how the existing diversity came about.

A historical perspective on evolving diversity in AEMs

The field of AEMs started with great expectations when the first mainframe computers were installed at universities in the 1960s (Lavington 1975). But because of the adaptive nature of living systems, making predictive AEMs proved to be more difficult than predicting the trajectory of a rocket to the moon.
This sparked the emergence of individual-based models sensu lato, including dynamic energy budget models (Kooijman 1993), structured population models (De Roos et al. 1992) and individual-based models sensu stricto (Mooij and Boersma 1996), that zoom in on a particular (group of) species in the ecosystem. In an opposite direction, minimal dynamical models of ecosystems zoomed out to detect dominant nonlinearities in ecosystem responses to external forcing (Scheffer et al. 2001). Renewed interest in large ecosystem models occurred in the past decades, not the least as a result of the increased and distributed computational power, but this time with the tendency to link the models with individual-based and trait-based approaches (DeAngelis and Mooij 2005) and compare their behaviour with minimal dynamical models (Mooij et al. 2009). In the past, region-specific questions have led to region-specific models; however, as a result of current globalization, the need for widely applicable models and models covering regional or continental aspects is rapidly increasing. The growing recognition of the importance anthropogenic stressors on ecosystems and the services provided by ecosystems asks for coupling of ecological models with socio-economics models (e.g. Downing et al. 2014). This can be realized by using output of one model as input for the other model, or run-time exchange of input and output between such models. The latter method is more complicated and only becomes necessary when there are strong feedbacks between ecology and socio-economics.

Arguments for reducing diversity

There are valid arguments why aquatic ecology as a whole could benefit from streamlining the diversity in AEMs. First, some formulations have been shown to be both less accurate and more complex than alternatives (Tian 2006). Second, some models are developed to answer one specific question and thus lose their functionality once this question has been addressed. It is likely that this kind of models has a high turnover rate, but such models could also be incorporated in large models as the results prove to be relevant. Finally, the presence of pseudo-diversity is an argument to reduce the number of models. For example, in climate studies, it has been shown that the performance of ensemble models significantly improved when pseudo-diversity was reduced (Knutti et al. 2013). Ideally, groups that work in parallel on similar models should have the incentives to join efforts, but these incentives are often not in place. Also at the level of the individual scientists, there seem to be few, if any, incentives to give up one’s own model, whereas there are many incentives to maintain it or even start yet another one. Only when the incentives that lead to fragmentation are overcome, or are outweighed by incentives to join forces, can we expect a healthy consolidation of the field to take place. Frameworks such as Delft3D-Delwaq (Deltares 2014), FABM (Bruggeman and Bolding 2014) and DATM (Mooij et al. 2014) facilitate this process, but also these frameworks have the risk to be duplicated, leading to yet another layer of fragmentation. The turnover rate of AEMs is hard to measure since publications on dropped models are rare, if they even exist. At the same time, the absence of publications on a specific model does not necessarily mean that a model became unused, as engineers, for example, might use the specific model on a daily basis without publishing the results. Furthermore, unlike extinct species that reduce biodiversity, ‘dead’ models can become ‘alive’ when a need for their existence emerges, thereby contributing again to model diversity.

Arguments for enlarging diversity

Because the field of aquatic ecosystem modelling can appear quite fragmented, arguments for enlarging diversity in AEMs are easily overlooked. Nevertheless, there should always be room for good ideas and new avenues. An interesting example is provided by minimal dynamical models. When these became prominent in the shallow lake literature about 25 years ago, they were met with considerable reservation and hardly perceived as a step forward. Nowadays, their ability to illustrate and communicate essential nonlinearity in the response of ecosystem (and many other dynamical systems) is broadly recognized (Scheffer et al. 2001). Another emerging approach with many applications in the aquatic domain is Dynamic Energy Budgets (DEB) (Kooijman 1993). The scope of current DEB models, however, is too limited to be qualified as ecosystem models as defined in this study.

Arguments for conserving diversity

With the first generation of aquatic ecosystem modellers about to retire, there can be serious concern about
a loss of useful models and approaches, requiring active conservation effort by the community at large. Proper implementation of conservation schemes will help to prevent the proverbial ‘reinvention of the wheel’ (Mooij et al. 2010). Additionally, it can help future model developers to anticipate what models and formulations worked well and which did not. Obviously, this learning process is hampered at the lack of documentation of failures in the scientific literature. Conserving diversity would thus have a great educational value and would help understand the ‘genealogy’ of the existing models. Conservation of model diversity is important for science as well, as science builds on repetition which only can be complied with when code is conserved. However, model diversity conservation has to overcome ‘code rot’, which is the deterioration of software as a result of the ever evolving modelling environment, making the software invalid or unusable (Scherlis 1996). To prevent code rot, the code should be maintained. Another option is to conserve models in their purest mathematical form (e.g. like in the concept behind DATM, Mooij et al. 2010).

How to facilitate evolving diversity

One would like to have tools available and mechanisms in place that would allow diversity to evolve through a ‘natural selection’ of models. Natural selection is an emergent property of a system in which there is variation among agents; this variation is transferred to the offspring of the agents and has an impact on the survival of the agents. We have shown that there is ample diversity among AEMs, and there seems to be a healthy cross-fertilization of ideas leading to continued development of new versions and models. What may be hampering ‘natural selection’ among AEMs, however, are standardized methods to compare model ‘fitness’ within their niche and given the research question they address. Here, we point specifically to the research question since models might have a different purpose, and it only makes sense to compare the fitness of those models that are able to answer the same research question. To enhance selection and ‘gene transfer’, easy model accessibility is necessary in the first place. Easy accessibility not only includes freely available model software but also low time costs of, for instance, learning new modelling code or approaches. Additionally, data availability is very important for the improvement of models (Hipsey et al. 2015). As long as models are inaccessible, due to, for example, licence restrictions or inappropriate manuals, modellers will most likely choose the models in use by their colleagues (see Online Resource 2). These easily accessible models may not be the best suitable to answer their questions. Secondly, standard objective assessment criteria to calibrate and validate models are important (Refsgaard et al. 2005; Robson 2014b). These criteria are different for each modelling niche, as models that are suitable, for example, for forecasting of algal blooms require other criteria than models suitable for biodiversity assessments. It also implies providing a freely accessible set of data used as calibration or validation data (meteorology, hydrology, hydrodynamics, nutrient fluxes, etc.) of the models to be benchmarked. The application of the models to these common test data enables a direct comparison without interfering effects from differences in basin morphometry, hydrology, meteorology, and so on. The main idea behind this benchmarking is not to classify models into ‘good’ and ‘bad’ ones, but instead to characterize the dynamic behaviour and specific abilities of the separate models. Finally, we would like to point to the importance of the conservation and maintenance of expertise and experience for model evolution. Currently, project life cycles are generally short, and while mobility of people can help to spread models, the same mobility could lead to a local loss of expertise (Herrera et al. 2010; Parise et al. 2012).

Discussion

How can biodiversity research help us to interpret model diversity?

One could see the myriad of model purposes as niches that shape model diversity. Like biodiversity, model diversity can be organized in taxonomic structures to classify models. Using Wikipedia as a reference, such a taxonomic study has been done already for programming languages and showed a phylogenetic tree with new programming languages emerging from different elements of earlier programming languages (Valverde and Solé 2015). A similar study for AEMs is intriguing, but is beyond this study. Our analysis revealed a large diversity in the models. We argue that to fully exploit the niche, the tools for analysis provided in each modelling framework should be used. If we divide the AEMs in specialists or

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generalists, the majority of the AEMs seem to be specialists that address the research question that led to their development but with little application beyond. This can be attributed to the fact that models are often locked within frameworks which obstruct communication and cross-fertilization between the models (Mooij et al. 2014). For the same reason, we could question whether there is enough competition between the models to enable survival of the fittest and thus competitive exclusion. At present, most models seem to have the fingerprints of the resource group it is developed in, as if they were species that evolved in their island-specific supported niche. This has the disadvantage of reinventing the wheel, but surely has its advantage as well since the independently evolved models can be used for comparison as in ensemble modelling.

Recommendations

Our analysis of exploring, exploiting and evolving diversity in AEMs leads us to three types of recommendations related to (1) availability, (2) standardization and (3) coupling of AEMs.

Availability of AEMs

With respect to the availability of AEMs, it is important to continue the current trend of open-source policies for AEM models, tools for analysis and data. This will increase the transparency of model structure, assumptions and approaches. Besides that, there is an urgent need for a public overview of existing AEMs. This could be a Wikipedia list, with links to relevant (online) documentation or similar initiatives. Such a list could be complemented with an overview of the forces and niches that created the existing diversity in AEMs. Once there is an overview of the niches in which models are designed, the suitability of models for other applications is better assessed. Documentation of the available AEMs will create awareness of the full width of approaches in AEMs to avoid tunnel vision. We should also actively preserve AEMs to learn from the past and thereby avoid reinventing the wheel but also to identify and prevent pseudo-diversity in AEMs.

Standardization of AEM practices

We recommend developing standardization in the documentation of AEMs [comparable with, e.g. ODD for IBM's, Grimm et al. (2006)], terminology to categorize AEMs and the methods to analyse AEMs. Standardization of documentation and terminology is desirable for the communication on the different available models. Standardization of methods for parametrization, comparison, calibration, testing, structuring, conversion and interpolation in AEMs will lead to a common practice in model analysis.

Linking AEMs

In our analysis, we compared models by their state variables, while additional diversity is hidden in the process formulations. Here, we recommend fulfilling the next step by comparing models by their process formulations. Currently, this step is a time-consuming and difficult task as a result of lack in the availability of model definitions. Perhaps this step will be possible in the future due to the emerging linking approaches such as DATM. And linking has more benefits. We advocate linking AEMs with models from other disciplines to answer questions that require a holistic approach. We recommend running AEMs in more than one spatial setting to gain more insight into the effects within the spatial context and suggest running a given AEM in multiple frameworks to use the full set of tools for analysis and advice of the user community. Finally, we recommend ensemble modelling with AEMs in order to use the best out of multiple models. For example, statistical- and process-based AEMs should be used side by side because they have complementary strengths.

We anticipate that increasing model availability, standardization of model documentation, and various forms of linking will lead to an evolving diversity of AEMs in which the better performing models outcompete the poorer performing models. Given the large number of model niches, however, there will always remain a great diversity in AEMs.

Perspectives

We can only speculate where the field of aquatic ecosystem modelling will be heading in the coming five to 10 years. We expect that many new developments will be triggered and enabled by general trends in science, technology and society. Here, we list 10 of these possible trends. (1) We expect that wikis (e.g. Wikipedia), where users can either retrieve information
or contribute information through standardized web interfaces, will gain in importance for the documentation and distribution of AEMs. While we recognize the inherent lack of quality control, we highly value the ease of access, the community effort and dynamic nature of this approach (the name ‘wiki’ is derived from the Hawaiian word for ‘quick’). (2) We recognize initiatives to develop e-infrastructures for the implementation of AEMs and other environmental models where users of different levels of experience share easy and secure access to models and data according to their needs. (3) We envision that current trends in the mandatory storage of scientific data in repositories will be extended to model code. (4) We envision that online databases of model parameters will be developed and become an important resource for the development and improvement of AEMs. (5) We see a change from the way consultancy companies earn money with AEMs. Formerly, their business model was based on copyrights of model code. Formerly, their business model was based on copyrights of model code. Now, we see a switch to a business model emerging that is based on expertise in applying open-source models. (6) We hope for a further integration of the development, analysis and application of AEMs in fundamental research and applied science. It will be a challenge to develop models of intermediate complexity that are simple enough to be thoroughly analysed, yet complex enough to be applicable in real-life cases. (7) We hope for a better coverage of the mutual interaction of ecosystem dynamics and biodiversity in AEMs. (8) We expect that the domain of model application (e.g. type of water, climate zone and stress factors) of AEMs will increase. In the end, this will allow for global analysis of aquatic ecosystems exposed to multiple stressors. (9) We envision the implementation of AEMs in apps that run in a local context (e.g. using GPS information) on a smartphone or tablet computer. (10) Finally, we expect that various forms of ensemble modelling will gain importance. Through a comparative evaluation of model performance, ensemble modelling can contribute to a ‘natural selection’ of AEMs within their niches that are defined by questions from society and science.

**Text Box 1** Glossary of terms related to aquatic ecosystem modelling. This glossary can also be found in database format in Online Resource 1, Datasheet 1. For each term, an acronym and a description, followed by, in so far known to us, a Wikipedia page, a homepage or other relevant web pages and one or more key publications is given, using the following style: **Term (Acronym):** Definition of term (Wikipedia | Web page | Publication)

**ACSL** *(Advanced Continuous Simulation Language)*: A computer language with user interface and analysis tools for the implementation of sets of ordinary differential equations. ([http://en.wikipedia.org/wiki/Advanced_Continuous_Simulation_Language](http://en.wikipedia.org/wiki/Advanced_Continuous_Simulation_Language) | [http://www.acslx.com](http://www.acslx.com)).

**ADCIRC** *(ADvanced CIRCulation Model)*: A model for storm surge, flooding and larvae drift. ([http://adcirc.org](http://adcirc.org)).

**AED in FABM** *(Aquatic EcoDynamics modelling library)*: A configurable library of biogeochemical model components including oxygen, nutrients, phytoplankton, zooplankton and sediment implemented in FABM. ([http://aed.see.uwa.edu.au/research/models/AED](http://aed.see.uwa.edu.au/research/models/AED), [http://sf.net/p/fabm](http://sf.net/p/fabm) | Bruce et al. 2014).

**AEM** *(Aquatic Ecosystem Model)*: A formal procedure by which the impact of external or internal forcing on aquatic ecosystem states can be estimated. In sometimes used as a synonym for water quality model. ([http://en.wikipedia.org/wiki/Aquatic_ecosystem](http://en.wikipedia.org/wiki/Aquatic_ecosystem), [http://en.wikipedia.org/wiki/Ecosystem_model](http://en.wikipedia.org/wiki/Ecosystem_model), [http://en.wikipedia.org/wiki/Water_quality_modelling](http://en.wikipedia.org/wiki/Water_quality_modelling) | Mooij et al. 2010).

**AEMON** *(Aquatic Ecosystem MOdelling Network)*: A grass roots network of aquatic ecosystem modellers that aims for sharing knowledge, accelerating progress and improving models. ([https://sites.google.com/site/aquaticmodelling](https://sites.google.com/site/aquaticmodelling)).

**Agent-based model** (): A modelling format used in individual-based models. ([http://en.wikipedia.org/wiki/Agent-based_model](http://en.wikipedia.org/wiki/Agent-based_model) | DeAngelis and Mooij 2005).

**Algorithmic uncertainty** (): A misestimate of the data by the model’s output as result of errors made by the numerical integration method that is used. ([http://en.wikipedia.org/wiki/Uncertainty_quantification](http://en.wikipedia.org/wiki/Uncertainty_quantification) | ).

**AQUASIM** (): A modelling framework for the implementation of AEMs in pre-defined compartment types. ([http://www.eawag.ch/en/department/siam/software](http://www.eawag.ch/en/department/siam/software) | Reichert 1994).

**AQUATOX** (): An AEM that predicts the fate of various pollutants. ([http://www.epa.gov/athens/wwqtsc/html/aquatox.html](http://www.epa.gov/athens/wwqtsc/html/aquatox.html) | Park et al. 2008).

**ASM2d** *(Activated Sludge Model no. 2D)*: A model for biological phosphorus removal with simultaneous nitrification–denitrification in activated sludge systems. ([https://build.openmodelica.org/Documentation/WasteWater.ASM2d.html](https://build.openmodelica.org/Documentation/WasteWater.ASM2d.html) | Henze et al. 1999).
Text Box 1 continued

**Aster2000 (modified ASTERionella formosa model):** An AEM for reservoirs. (Thébault 2004).

**ATLANTIS**: A flexible, modular modelling framework for developing AEMs that aims to consider all aspects of a marine ecosystem, including biophysical, economic and social aspects. (http://atlantis.cmar.csiro.au | Fulton et al. 2007, 2011).

**BaltWeb**: An application of the model LakeWeb to the Baltic Sea. (Håkanson and Gyllenhammar 2005).

**BELAMO in AQUASIM (Biogeochemical Ecological LAke MOdel in AQUASIM)**: A biogeochemical and ecological lake model implemented in AQUASIM which allows flexible modifications of the differential equations. (Reichert 1994; Omlin et al. 2001).

**BELAMO in R (Biogeochemical Ecological LAke MOdel in R)**: A biogeochemical and ecological lake model implemented in R which allows flexible modifications of the differential equations. (Reichert 1994; Omlin et al. 2001).

**Bifurcation analysis** (Box model): A mathematical analysis technique that aims for identifying qualitative shift in model behaviour, e.g. stable versus unstable, in response to internal or external forcing to the model. Extensively used in theoretical ecology, but much less so in the analysis of AEMs, despite its potential to reveal general response curves of the model such as those depicted in Fig. 1. (http://en.wikipedia.org/wiki/Catastrophe_theory | Scheffer et al. 2001).

**Biogeochemical model** (BLOOM II): A phytoplankton community model that uses linear programming, an optimization technique, to calculate the maximum biomass that can be obtained given the available amount of nutrients and constraints on growth and mortality. (Los 1991).

**BNN-EQR (Bayesian Belief Network model for Ecological Quality Ratio)**: A statistical model relating Ecological Quality Ratio as defined in the Water Framework Directive in lakes and rivers to abiotic and management factors. (Gobeyn 2012).

**Box model**: A representation of a complex system in the form of boxes or reservoirs linked by fluxes. (http://en.wikipedia.org/wiki/Climate_model#Box_models).

**BRNS (Biogeochemical Reaction Network Simulator)**: A simulation environment in which transport processes are interfaced with relevant biogeochemical reactions for sediment diagenesis. (http://www.geo.uu.nl/Research/Geochemistry/RTM_web/project1.htm | Aguilera et al. 2005).

**BROM (Bottom RedOx Model)**: A water–sediment column model of elemental cycles, redox chemistry and plankton dynamics. (Yakushev et al. 2014).

**C (general-purpose procedural programming language)**: (http://en.wikipedia.org/wiki/C_(programming_language)).

**C++ (general-purpose object-oriented programming language)**: (http://en.wikipedia.org/wiki/C%2B%2B).

**CAEDYM (Computational Aquatic Ecosystem DYNAmics Model)**: A complex ecological and biogeochemical model that can be coupled with the hydrodynamic drivers DYRESM or ELCOM. (http://www.cwr.uwa.edu.au/software1/models1.php?mfid=3 | Hipsey et al. 2006).

**Calibration**: - (See Model calibration).

**Cartesian grid**: - (See Cubic grid).

**Catastrophic shift**: - (See Regime shift).

**CCHE1D-WQ, CCHE2D-WQ, CCHE3D-WQ (Center for Computational Hydroscience and Engineering 1D/2D/3D Water Quality model)**: A model that simulates water quality processes in river channels, streams, lakes and coastal waters in a 1D, 2D or 3D setting. (http://www.ncche.olemiss.edu/research/basic/water).

**CE-QUAL-W2 (Corps of Engineers water QUALity model Width averaged 2d)**: A two-dimensional longitudinal/vertical hydrodynamic and water quality model for reservoirs/lakes, rivers and estuaries that includes full eutrophication modelling state variables including sediment diagenesis, algae, zooplankton, and macrophytes. (http://www.ce-pdx.edu/w2, http://www.cequalw2wiki.com/Main_Page | Cole and Wells 2003).

**Charisma**: An individual-based macrophyte community model. (http://www.projectenaew.wur.nl/charisma | Van Nes et al. 2002b).

**CLI (Command Line Interface)**: A way of controlling a computer or program by entering text messages at a command line. The computer or program responds with text but also with graphical output. (http://en.wikipedia.org/wiki/Command-line_interface).

**COASTMAB (COASTal MASS Balance model)**: A dynamic model for coastal water quality based on LakeMab. (Håkanson and Eklund 2007).

**Code rot**: A deterioration of software as a result of the ever evolving environment, making the software invalid or unusable. (http://en.wikipedia.org/wiki/Software_rot | Scherlis 1996).
Text Box 1 continued

**Code verification**: A substantiation that a model code is in some sense a true representation of a conceptual model within certain specified limits or ranges of application and corresponding ranges of accuracy. (Refsgaard and Henriksen 2004).

COHERENS (COupled Hydrodynamical-Ecological model for REgioNal and Shelf seas): A hydrodynamic driver available in FABM. (http://odnature.naturalsciences.be/coherens/about).

**Community model**: A model of closely interacting species within an ecosystem. (http://en.wikipedia.org/wiki/Community_%28Ecology%29).

**Compartment model**: A model of competing species within an ecosystem. (http://en.wikipedia.org/wiki/Compartment_model).

**Complex dynamic model**: A dynamic model with many components. One way to further define this concept would be as those dynamical models that are too complex to be analysed with analytical techniques. See also Minimal dynamic model. (http://en.wikipedia.org/wiki/Mathematical_model#Complexity).

**Conceptual model**: A description of reality in terms of verbal descriptions, equations, governing relationships or natural laws that purport to describe reality. (http://en.wikipedia.org/wiki/Conceptual_model).

**Consumer-resource model**: A model of two or more species that interact with each other through predation, competition, parasitism, mutualism, etc. (http://en.wikipedia.org/wiki/Consumer-resource_systems).

**Cubic grid**: A n-dimensional regular grid consisting of unit squares or cubes. (http://en.wikipedia.org/wiki/Regular_grid).

**Curvilinear grid**: A n-dimensional regular grid with cuboidal cell structure. (http://en.wikipedia.org/wiki/Regular_grid).

**DATM (Database Approach to Modelling)**: An approach in which a model is specified in mathematical terms in a database. To create a running instance of a model, framework-specific code is generated with automated code generators. (Mooij et al. 2014).

**DEB (Dynamic Energy Budgets)**: An approach that captures the elementary energy allocation within an organism and the consequences thereof for growth and reproduction. (http://www.bio.vu.nl/thb/deb).

**Delft3D**: A modelling suite for 1D, 2D and 3D hydrologic, hydrodynamic, hydraulic and water quality models. (http://www.deltaresystems.com/hydro/product/621497/delft3d-flow).

**Delft3D-DELWAQ**: A component of the Delft3D 4 Suite that estimates the dynamic spatial concentration distribution of individual particles by following their tracks in time. The waste substances may be conservative or subject to a process of simple, first-order decay; a typical application is oil spill modelling. (http://oss.deltares.nl/web/delft3d/delwaq).

**Delft3D-Flexible Mesh**: A 1D/2D/3D hydrodynamic program of the Delft3D 4 Suite to simulate non-steady flows in relatively shallow water. It incorporates the effects of tides, winds, air pressure, density differences, waves, turbulence and drying and flooding. (http://oss.deltares.nl/web/delft3d/manuals).

**Delft3D-MOR**: A component of the Delft3D 4 Suite that computes sediment transport and morphological changes for an arbitrary number of cohesive and non-cohesive fractions. Both currents and waves act as driving forces, and a wide variety of transport formulae have been incorporated. (http://oss.deltares.nl/web/delft3d/manuals).

**Delft3D-PART**: A component of the Delft3D 4 Suite that estimates the dynamic spatial concentration distribution of individual particles by following their tracks in time. The waste substances may be conservative or subject to a process of simple, first-order decay; a typical application is oil spill modelling. (http://oss.deltares.nl/web/delft3d/manuals).

**Delft3D-SED**: A subset of the DELWAQ process library for short- or medium-term—days, weeks, months—cohesive and non-cohesive sediment transport. (http://oss.deltares.nl/web/delft3d/manuals).

**Delft3D-WAQ (incl GEM/BLOOM/ECO)**: A component of the Delft3D 4 Suite that simulates the far and mid-field water and sediment quality due to a variety of transport and water quality processes. To accommodate these, it includes several advection diffusion solvers and an extensive library of process formulations for user-selected substances. (http://oss.deltares.nl/web/delft3d/manuals).

**Delft3D-WAVE**: A component of the Delft3D 4 Suite that computes the non-steady propagation of short-crested waves over an uneven bottom, considering wind action, energy dissipation due to bottom friction, wave breaking, refraction, shoaling and directional spreading. The programme is based on the spectral model SWAN. (http://oss.deltares.nl/web/delft3d/manuals).

**Delphi**: An object-oriented programming language based on pascal. (http://en.wikipedia.org/wiki/Delphi_(programming_language)).

**Delta Shell**: A modelling framework for developing and analysing environmental models to simulate water, soil and the subsurface processes. (http://oss.deltares.nl/web/delta-shell).
**deSolve (R package):** A set of general solvers for initial value problems of Ordinary Differential Equations, Partial Differential Equations, Differential Algebraic Equations and Delay Differential Equations. (https://cran.r-project.org/web/packages/deSolve | Soetaert et al. 2010).

**DIECAST (DIEtrich Center for Air Sea Technology):** A hydrodynamic model. (http://efdl.as.ntu.edu.tw/research/diecast).

**Domain of applicability of conceptual model:** A prescribed set of conditions for which the conceptual model has been tested, i.e. compared with reality to the extent possible and judged suitable for use by model confirmation. (Refsgaard and Henriksen 2004).

**Domain of applicability of model:** A prescribed set of conditions for which the site-specific model has been tested, i.e. compared with reality to the extent possible and judged suitable for use by model validation. (Refsgaard and Henriksen 2004).

**Domain of applicability of model code:** A prescribed set of conditions for which the model code has been tested, i.e. compared with analytical solutions, other model codes or similar to the extent possible and judged suitable for use by code verification. (Refsgaard and Henriksen 2004).

**DUFLOW (DUTch FLOW model):** A modelling suite for the simulation of non-stationary 1D hydrodynamics and water quality processes. (http://www.mx-groep.nl/duflow).

**DUPROL (DUTch PROgramming Language):** A computer language for the implementation of the water quality processes in DUFLOW. (http://www.mx-groep.nl/duflow).

**Dynamic model:** A mathematical model that captures the development of the system through time as opposed to a static model. (http://en.wikipedia.org/wiki/Mathematical_model).

**DYRESM (DYnamic REservoir Simulation Model):** A 1D hydrodynamic model for predicting the vertical distribution of temperature, salinity and density in lakes and reservoirs. DYRESM coupled with CAEDYM. (http://www.cwr.uwa.edu.au/software1/models1.php?mid=2 | Hamilton and Schladow 1997).

**Ecopath with Ecosim:** A software package for balancing food web interactions, calculating network characteristics and assessing the impact of fishing on the food web. (http://en.wikipedia.org/wiki/Ecopath | http://www.ecopath.org | Christensen and Pauly 1992).

**Ecosystem model:** An abstract, usually mathematical, model of an ecological system which is developed and analysed to understand and predict the dynamics of the real system. (http://en.wikipedia.org/wiki/Ecosystem_model).

**ECOWASP (ECOsystemmodel for WAdden Sea Project):** A dynamic model for the integrated simulation of biological, chemical, and physical processes in shallow tidal water systems. (Brinkman et al. 2001).

**EEMOD_DNSMOD (Detailed Nitrogen Sediment MODel inside of an Essential Ecological MODel):** An aquatic nitrogen cycle model including a layered sediment compartment. (http://sourceforge.net/projects/eemoddnsmod).

**EFDC (Environmental Fluid Dynamics Code):** A hydrodynamic model that can be used to simulate aquatic systems in one, two, or three dimensions and that can be coupled with WASP. (http://en.wikipedia.org/wiki/EFDC_Explorer | http://www.epa.gov/athens/wwqtsc/html/efdc.html | Hamrick and Wu 1997; Wu et al. 1997).

**ELCOM (Estuary, Lake and Coastal Ocean Model):** A 3D finite-difference baroclinic hydrodynamic model to simulate stratified waters bodies with environmental forcing. ELCOM can be coupled with CAEDYM. (http://www.cwr.uwa.edu.au/software1/models1.php?mid=5 | Robson and Hamilton 2004).

**ELISE:** A software interface to couple results of a hydrodynamic model with biological equations in a box-model representation. (Ménésguen 1991).

**EMS (Environmental Modelling Suite):** A modelling suite consisting of a hydrodynamic model SHOC, a sediment dynamic model MECOSED and an ecological/biogeochemical model. EMS is optimized for coastal systems. (http://www.emg.cmar.csiro.au/www/en/emg/software/EMS.html | Skerratt et al. 2013).

**Ensemble technique:** A forecasting technique where certain aspects of modelling processes are duplicated. Examples of ensemble techniques are the use of multiple models, multiple model inputs or multiple integration schemes. (http://en.wikipedia.org/wiki/Ensemble_forecasting).

**Environmental niche model:** A model that predicts the distribution of a species in its geographic space on the basis of the distribution of its environmental requirements. (http://en.wikipedia.org/wiki/Environmental_niche_modelling).

**ERGOM (Ecological ReGional Ocean Model):** A semi complex NPZD type of model with cyanobacteria. (http://www.ergom.net | Neumann 2000; Neumann et al. 2002).

**ERSEM (European Regional Seas Ecosystem Model):** A marine AEM. (http://www.meece.eu/library/ersem.html | Baretta et al. 1995).

**ESMF (Earth System Modelling Framework):** An interface between various hydrodynamic and water quality process formulations. (http://www.earthsystemmodeling.org/about_us, http://sourceforge.net/p/esmf/esmf/ci/master/tree).
Euler integration (): A simple way to integrate ordinary differential equations that bears similarity with difference equations but is fundamentally different because it aims for describing a continuous process. (http://en.wikipedia.org/wiki/Euler_method).

**eWater Source ():** A model that is designed to simulate all aspects of water resource systems to support integrated planning, operations and governance from urban, catchment to river basin scales including human and ecological influences. (http://en.wikipedia.org/wiki/EWater) (http://ewater.com.au/products/ewater-source, http://www.toolkit.net.au/tools/Source%20public%20version%29 Argent et al. 2009).

**Experimental uncertainty ():** A measure of errors in observational data. (http://en.wikipedia.org/wiki/Uncertainty_quantification).

**FABM (Framework for Aquatic Biogeochemical Models):** An interface between various hydrodynamic and water quality process formulations. (http://fabm.sourceforge.net).

**FEMME (Flexible Environment for Mathematically Modelling the Environment):** A modelling framework for the implementation of AEMs. (Soetaert et al. 2002).

**Finite Element ():** A numerical technique to solve boundary problems by subdividing the domain in simpler subdomains—finite elements—in order to approximate the exact solution. (http://en.wikipedia.org/wiki/Finite_element_method Hrennikoff 1941).

**FLAKE (Freshwater LAKE model):** A freshwater lake model for predicting vertical temperature distribution and mixing conditions. (http://www.flake.igb-berlin.de Mironov 2008).

**Flexible Mesh ():** An unstructured grid in 1D, 2D or 3D consisting of different geometric shapes within one mesh. (http://oss.deltares.nl/web/delft3dfm).

**FME (Flexible Modelling Environment, R implementation of FEMME):** A flexible modelling framework for inverse modelling, sensitivity, identifiability, Monte Carlo analysis. (http://cran.r-project.org/package=FME Soetaert and Petzoldt 2010).

**Foodweb model ():** A model of species within an ecosystem that are linked by trophic interactions. (http://en.wikipedia.org/wiki/Food_web).

**FORTRAN (FORmula TRANslation system):** A general-purpose procedural programming language with object-oriented extensions. (http://en.wikipedia.org/wiki/Fortran).

**Framework ():** (See Modelling framework).

**Functional programming ():** A programming paradigm that treats computation as the evaluation of mathematical functions. Functional programming is focused on describing what should be calculated rather than how it should be calculated. (http://en.wikipedia.org/wiki/Functional_programming).

**FVCOM (Finite Volume Community Ocean Model):** An unstructured grid, finite-volume, 3D primitive equation, turbulent closure coastal ocean model. (http://en.wikipedia.org/wiki/Finite_Volume_Community_Ocean_Model Chen et al. 2006).

**GEMSS (Generalized Environmental Modeling System for Surfacewaters):** An integrated system of 3D hydrodynamic and transport modules embedded in a geographic information and environmental data system. (http://en.wikipedia.org/wiki/Generalized_Environmental_Modeling_System_for_Surfacewaters).

**Generalized Lotka-Volterra model ():** A multidimensional implementation of the Lotka-Volterra competition and predation equations, typically with linear interaction terms. (http://en.wikipedia.org/wiki/Generalized_Lotka%E2%80%93Volterra_equation).

**GETM (General Estuarine Transport Model):** A structured grid 3D hydrodynamic model that can be coupled with FABM. (http://www.getm.eu).

**GLEON (Global Lake Ecological Observatory Network):** A transdisciplinary network that aims at sharing and interpreting high-resolution sensor data from different lakes worldwide. (http://www.gleon.org).

**GLM (General Lake Model):** A 1D Lake and Wetland hydrodynamic model that simulates the balance of water, salt and heat, including vertical stratification. (http://aed.see.uwa.edu.au/research/models/GLM Hipsey et al. 2013).

**GLOBIO-AQUATIC ():** An empirically based model of biodiversity intactness and species richness as a function of main abiotic drivers. (http://www.globio.info Janse et al. 2014, 2015).

**GLUES (Global Land Use and technological Evolution Simulator):** A model used for land-use and socio-technological evolution simulations. (http://sf.net/p/glues Lemmen et al. 2011; Lemmen and Wirtz 2014).

**GOTM (General Ocean Turbulence Model):** A 1D water column model with focus on vertical mixing that can be coupled with FABM. (http://www.gotm.net).

**GPL (GNU General Public Licence):** An open-source software licence. (http://en.wikipedia.org/wiki/GNU_General_Public_License).
Text Box 1 continued

**GRIND for MATLAB** (): A modelling framework based on MATLAB. ([http://www.sparcs-center.org/grind](http://www.sparcs-center.org/grind)).

**Guam Atlantis Coral Reef Ecosystem Model** (): An evaluation and management strategy tool used particularly for simulating management policies and methods for coral reef conservation and assessment. ([http://www.pifsc.noaa.gov/cred/guam_atlantis_ecosystem_model.php](http://www.pifsc.noaa.gov/cred/guam_atlantis_ecosystem_model.php)).

**GUI (Graphical User Interface)**: A communication tool with graphical icons to enable interaction between the electronic device and the user. ([http://en.wikipedia.org/wiki/Graphical_user_interface](http://en.wikipedia.org/wiki/Graphical_user_interface)).

**HABITAT**: A spatial analysis tool to analyse the availability and quality of habitats for individual or groups of species. ([https://publicwiki.deltares.nl/display/HBTHOME/Home](https://publicwiki.deltares.nl/display/HBTHOME/Home) | Haasnoot and Van de Wolfshaar 2009).

**HBV (Hydrologiska Byråns Vattenbalansavdelning model)**: A catchment hydrological model simulating river discharges and solute transport in the rivers and catchments. ([http://en.wikipedia.org/wiki/HBV_hydrology_model](http://en.wikipedia.org/wiki/HBV_hydrology_model) | http://www.smhi.se/forskning/forskningsomraden/hydrologi/hbv-1.1566 | Bergström 1976).

**HEC-RAS (Hydrologic Engineering Center River Analysis System)**: A hydraulic model for engineering of pipes and canals and rivers, which has also modules for basic water quality. ([http://en.wikipedia.org/wiki/HEC-RAS, http://www.hec.usace.army.mil/software/hec-ras](http://en.wikipedia.org/wiki/HEC-RAS, http://www.hec.usace.army.mil/software/hec-ras) | Brunner 2001).

**Hydraulic model**: A model describing fluid mechanics including power generation and distribution. ([http://en.wikipedia.org/wiki/Hydraulics](http://en.wikipedia.org/wiki/Hydraulics)).

**Hydrodynamic model**: A model describing motion of water. ([http://en.wikipedia.org/wiki/Fluid_dynamics](http://en.wikipedia.org/wiki/Fluid_dynamics)).

**Hydrological model**: A model describing the water cycle. ([http://en.wikipedia.org/wiki/Hydrology](http://en.wikipedia.org/wiki/Hydrology), [http://en.wikipedia.org/wiki/Hydrological_transport_model](http://en.wikipedia.org/wiki/Hydrological_transport_model)).

**IBM (Individual-based model)**: An ecological model, build on the basis of traits, physiology and behaviour of interacting individuals. ([http://en.wikipedia.org/wiki/Agent-based_model](http://en.wikipedia.org/wiki/Agent-based_model) | DeAngelis and Mooij 2005).

**IDE (Integrated development environment)**: A software application that provides comprehensive facilities to computer programmers for software development. ([http://en.wikipedia.org/wiki/Integrated_development_environment](http://en.wikipedia.org/wiki/Integrated_development_environment)).

**Identifiability**: A property of a model pointing at identical distribution of the data and the values of the model. Non-identifiable models can lead to differences in conclusions drawn based on the model values and observed data. ([http://en.wikipedia.org/wiki/Identifiability](http://en.wikipedia.org/wiki/Identifiability) | Huang 2005).

**IMAGE (Integrated Model to Assess the Global Environment)**: A global catchment nutrient model. ([http://themasites.pbl.nl/models/image](http://themasites.pbl.nl/models/image) | Moreé et al. 2013).

**Imperative programming**: A programming paradigm that describes computation in terms of statements that change a program state. Imperative programming is focused on describing how a program operates. ([http://en.wikipedia.org/wiki/Imperative_programming](http://en.wikipedia.org/wiki/Imperative_programming)).

**INCA (INtegrated CAtchment model)**: A process-based dynamic model for plant–soil system dynamics and in-stream biogeochemical and hydrological processes. ([http://www.reading.ac.uk/geographyandenvironmentalscience/research/INCA](http://www.reading.ac.uk/geographyandenvironmentalscience/research/INCA) | Wade et al. 2002).

**Interpolation uncertainty**: An unknown difference between model and reality as a result of calibration on different spatial or temporal data than the validation of the model. Whenever the validation falls out of the calibrated range, an interpolation uncertainty is introduced. ([http://en.wikipedia.org/wiki/Uncertainty_quantification](http://en.wikipedia.org/wiki/Uncertainty_quantification)).

**Inverse Modelling**: A technique used to infer from observations the causal factors that produced them. ([http://en.wikipedia.org/wiki/Inverse_problem](http://en.wikipedia.org/wiki/Inverse_problem)).

**InVitro**: An agent-based ecosystem-level management strategy evaluation modelling framework. ([http://www.cmar.csiro.au/research/mse/invitro.htm](http://www.cmar.csiro.au/research/mse/invitro.htm) | Fulton et al. 2011).

**JAVA**: A general-purpose object-oriented computer programming language that allows to run software applications under various operating systems without the need for recompilation. ([http://en.wikipedia.org/wiki/Java_%28programming_language%29](http://en.wikipedia.org/wiki/Java_%28programming_language%29)).

**JPJS (named after Jensen-Pedersen-Jeppesen-Søndergaard)**: A model for describing the recovery process after nutrient abatement. ([http://www.cmar.csiro.au/research/mse/invitro.htm](http://www.cmar.csiro.au/research/mse/invitro.htm) | Jensen et al. 2006).

**LAKE (from H. Baumert)**: A 1D hydrodynamic k-epsilon turbulence model that considers internal waves. ([http://www.hec.usace.army.mil/software/hec-ras](http://www.hec.usace.army.mil/software/hec-ras) | Baumert and Peters 2004).

**LAKE (from V. Stepanenko)**: A 1D hydrodynamic k-epsilon turbulence model capable of simulating methane. ([http://en.wikipedia.org/wiki/Imperative_programming](http://en.wikipedia.org/wiki/Imperative_programming) | Stepanenko et al. 2011, 2013).

**LAKEMAB (LAKE MAss Balance model)**: A dynamic model for lake water quality. ([http://www.hec.usace.army.mil/software/hec-ras](http://www.hec.usace.army.mil/software/hec-ras) | Bryhn and Håkanson 2007).
LAKEoneD (): A 1D hydrodynamic k-epsilon turbulence model with submodules for dissolved oxygen and a simple competition model for three functional phytoplankton groups. (I I Jöhnk and Umlauf 2001; Jöhnk et al. 2008).

LakeWeb (): A model to quantitatively describe the characteristic of lake food web interactions so that production and biomasses can be determined for the nine functional groups of organisms included in the model. (I I Håkanson and Bouillon 2003).

Lanier (): A network model based on EcoPATH, but using P as the currency. (I I Borrett and Osidede 2007).

LDE (Lattice differential equations): A set of spatially discrete ordinary differential equations. (I I Chow et al. 1996).

LGPL (GNU Lesser General Public Licence): An open-source software licence that is less strict than GPL. (http://en.wikipedia.org/wiki/GNU_Lesser_General_Public_License | http://www.gnu.org/licenses/lgpl.html |).

MARVL (MARine Virtual Lab): A suite of complex models, e.g. ocean circulation, waves, water quality, and marine biogeochemistry, a network of observing sensors, and a host of value-adding tools. (I http://www.marvl.org.au |).

Mass-balanced model (): A model that checks for the conservation of mass. (http://en.wikipedia.org/wiki/Mass_balance, http://en.wikipedia.org/wiki/Conservation_of_mass |).

Mathematica (): A computational software program. (http://en.wikipedia.org/wiki/Mathematica | http://www.wolfram.com/mathematica |).

MATLAB (): A numerical computation environment. (http://en.wikipedia.org/wiki/MATLAB | http://nl.mathworks.com/products/matlab |).

MATSEDLAB (): A MATLAB module for sediment diagenesis, carbon burial and bio-mixing. (I https://uwaterloo.ca/ecochemistry/software | Couture et al. 2010).

MECOSED (Model for Estuarine and COastal SEDiment transport): A model for estuarine and coastal transport. (I https://wiki.csiro.au/display/C2CCOP/EMS?MECOSED |).

MEDAWAR zone (): A conceptual zone depicting the area of problems which are most likely to produce fruitful results. Problems that are too simple are unlikely to produce novel or significant results. Problems that are too ambitious may not succeed at all or may be rejected by the research community at large. (http://en.wikipedia.org/wiki/Medawar_zone |).

Metamodel (): An abstraction of another model. (http://en.wikipedia.org/wiki/Metamodeling |).

Mike11 (after developer Mike Abbot): A 1D hydrodynamic and hydrological model for the simulation of rivers and channels. (http://en.wikipedia.org/wiki/MIKE_11 | http://www.mikepoweredbydhi.com/products/mike-11 | Nishat and Rahman 2009; Wijesekara et al. 2014).

Mike21 (after developer Mike Abbot): A 2D hydrodynamic model with flexible mesh for coastal and marine engineering and water quality applications. (http://en.wikipedia.org/wiki/MIKE_21 | http://www.mikepoweredbydhi.com/products/mike-21 | Appendini et al. 2013; Kaergaard and Fredsoe 2013).

Mike3 (after developer Mike Abbot): A 3D hydrodynamic model with flexible mesh for coastal and marine engineering and water quality applications. (http://en.wikipedia.org/wiki/MIKE_3 | http://www.mikepoweredbydhi.com/products/mike-3 | Passenko et al. 2008; Bolaños et al. 2014).

Mike-ECO Lab Eutrophication Model 1 (after developer Mike Abbot): An aquatic ecosystem modelling tool for use with Mike hydrodynamic drivers that includes several built-in ecosystem configurations and the ability to implement own equations. (I I Rasmussen et al. 2000; Hammrich and Schuster 2014).

Mike-FLOOD (): A toolbox for flood modelling. (http://en.wikipedia.org/wiki/MIKE_FLOOD | http://www.mikepoweredbydhi.com/products/mike-flood |).

Mike-SHE (after developer Mike Abbot—System Hydrologique European): A system for integrated catchment modelling, including groundwater, surface water, recharge and evapotranspiration. (http://en.wikipedia.org/wiki/MIKE_SHE | http://www.mikepoweredbydhi.com/products/mike-she | Refsgaard et al. 2010).

Minimal dynamic model (): A dynamic model with few components. One way to further define this concept would be as those dynamical models that are simple enough to be analysed with analytical techniques. See also Complex dynamic model. (http://en.wikipedia.org/wiki/Mathematical_model#Complexity |).

MINLAKE (): A 1D hydrodynamic model that includes dissolved oxygen. (I I Fang and Stefan 1996b, a; Stepanenko et al. 2013).

MIP (Model Intercomparison Project): A project to intercompare the output of multiple models using the same input data, i.e. an ensemble technique. Often used in climate and hydrologic research, sparse in aquatic ecosystem modelling. (I http://www.unige.ch/climate/lakemip |).

MME (Multi-Model Ensembles): A type of ensemble modelling in which a given problem is addressed concurrently with multiple models. (http://en.wikipedia.org/wiki/Ensemble_averaging |).
Text Box 1 continued

Model (): A knowledge domain-specific mathematical description of a study object, including input data and parameter values. An example of a knowledge domain is aquatic ecology. (http://en.wikipedia.org/wiki/Mathematical_model | Refsgaard and Henriksen 2004).

Model application (): A usage of a specific model for a specific case study. (Refsgaard and Henriksen 2004).

Model application domain (): A set of model applications that belong to a specific collection of model usages. An example of a model application domain is ‘eutrophication’. (Refsgaard and Henriksen 2004).

Model approach (): A modelling technique or method used to access a question. Examples of model approaches are mechanistic—e.g. trait-based, process-based—versus statistical—e.g. regression, neural network. (Refsgaard and Henriksen 2004).

Model calibration (): A procedure of adjustment of parameter values of a model to reproduce the response of reality within the range of accuracy specified in the performance criteria. (Refsgaard and Henriksen 2004).

Model code (): A mathematical formulation in the form of a computer program that is so generic that it, without program changes, can be used to establish a model with the same basic type of equations—but allowing different input variables and parameter values—for different study areas. (Refsgaard and Henriksen 2004).

Model confirmation (): A determination of adequacy of the conceptual model to provide an acceptable level of agreement for the domain of intended application. This is in other words the scientific confirmation of the theories/hypotheses included in the conceptual model. (Refsgaard and Henriksen 2004).

Model set-up (): An establishment of a site-specific model using a model code. This requires, among other things, the definition of boundary and initial conditions and parameter assessment from field and laboratory data. (Refsgaard and Henriksen 2004).

Model uncertainty (): A misestimate of the data by the model’s output. Model uncertainty has different origins as, for example, parameter uncertainty, structural uncertainty or algorithmic uncertainty. (Refsgaard and Henriksen 2004).

Model validation (): An approval that a model within its domain of applicability possesses a satisfactory range of accuracy consistent with the intended application of the model. (Refsgaard and Henriksen 2004).

Modelling environment (): A term that can refer to a modelling framework, an integrated development environment or a combination of both. (See IDE and Modelling framework).

Modelling framework (): A software package that can be combined with user-written code to create a software application. A key characteristic of a modelling framework, also referred to as a software framework, is that the framework calls the user-defined code. This distinguishes a modelling framework from a software library. Mostly, the framework itself cannot be modified by the user. (http://en.wikipedia.org/wiki/Software_framework | Mooij and Boersma 1996).

Modelling suite (): A set of interconnected models, mostly implemented in a common modelling framework. (https://www.deltares.nl/nl/software/delft3d-suite, http://www.mx-groep.nl/duflow, http://www.emg.cmar.csiro.au/www/en/emg/software/EMS.html, http://www.deltares.nl/en/software/sobek).

MOM (Modular Ocean Model): A 3D numerical ocean model based on the hydrostatic primitive equations. (http://en.wikipedia.org/wiki/Modular_ocean_model | http://mom-ocean.org/web | Griffies et al. 2005).

MONERIS (MOdelling Nutrient Emissions in RIver Systems): A catchment nutrient model. (http://www.icpdr.org/main/activities-projects/moneris-modelling-nutrient-emissions-river-systems).

MOSSCO (MOdular coupling System for Shelves and COasts): An interface between various hydrodynamical and water quality process formulations. (http://www.mossco.de).

Multi-compartment model (): A type of mathematical model used for describing the way materials or energies are transmitted among the compartments of a system. (http://en.wikipedia.org/wiki/Multi-compartment_model).

MUSIC (Model for Urban Stormwater Improvement Conceptualisation): A decision support system for storm-water quality management. (http://www.ewater.com.au/products/music).

Mylake (): A 1D model for lake physics and biogeochemistry suitable for uncertainty estimation and sensitivity analysis. (https://github.com/biogeochemistry/MyLake_public | Saloranta and Andersen 2007).

MyM (): An integrated environment for the development, visualization and application of simulations of dynamic systems. (http://www.my-m.eu | Beusen et al. 2011).

NEMO (Nucleus for European Modelling of the Ocean): A 3D modelling framework for oceanographic research, operational oceanography seasonal forecast and climate studies. (http://www.nemo-ocean.eu | Madec 2012).

NEMURO (North Pacific Ecosystem Model for Understanding Regional Oceanography): A model to simulate the dynamics of nutrient–phytoplankton–zooplankton food web in the ocean. (https://www.myroms.org/wiki/index.php/NEMURO_IN | Kishi et al. 2007).
Text Box 1 continued

NEMURO.FISH (North Pacific Ecosystem Model for Understanding Regional Oceanography with FISH module): An NEMURO model version extended with a fish module. (Janse et al. 2008, 2010).

NETLOGO (): A programmable modelling framework based on the LOGO programming language for developing agent-based models of natural and social phenomena with agent-based models. NET refers to the decentralized, interconnected nature of the phenomena that can be modelled. LOGO refers to the LOGO language of which a dialect is used. (http://en.wikipedia.org/wiki/NetLogo http://ccl.northwestern.edu/netlogo).

Neural network model (): A family of statistical learning models inspired by biological neural networks. (http://en.wikipedia.org/wiki/Artificial_neural_network).

NPZD model (Nutrient–Phytoplankton–Zooplankton–Detritus model): An AEM that focusses on the dynamics of nutrients, phytoplankton, zooplankton and detritus, thereby ignoring higher trophic levels. (http://fvcom.smast.umassd.edu/2014/01/17/2-research-npzd-model Heinele and Slawig 2013).

Numerical integration method (): A computational method to solve differential equations by approximating the integral. (http://en.wikipedia.org/wiki/Numerical_integration). PRESS et al. 1986).

Numerical recipes (): A book series and an extensive set of algorithms to perform various mathematical techniques, available in FORTRAN 77, FORTRAN 90, Pascal, C and C++. (http://www.nr.com).

Object-oriented programming (): A programming paradigm based on the concept of objects, which are data structures that contain data, in the form of fields, often known as attributes and code, in the form of procedures, often known as methods. (http://en.wikipedia.org/wiki/Object-oriented_programming).

ODD (Overview, Design concepts and Details): A format to document individual-based models. (Grimm et al. 2006).

ODE (Ordinary differential equations): A function or a set of functions of one independent variable and its derivatives. (http://en.wikipedia.org/wiki/Ordinary_differential_equations).

OMEXDIA in FABM (Ocean Margin EXchange and early DIAgenesis model): A model describing the dynamics of carbon, nitrogen and oxygen in marine sediments. (http://www.rforscience.com/modelling/omexdia Soetaert et al. 1996).

Optimization model (): A model in which—part of the—parameters are chosen such as to maximize or minimize a certain function, for instance the total amount of biomass. (http://en.wikipedia.org/wiki/Mathematical_optimization).

OSIRIS (Object-oriented Simulation Framework for Individual-based Simulations): A set of C++ routines that assist the development of ecological simulation models, including individual-based models. (Mooij and Boersma 1996).

PCDitch in ACSL/GRIND for MATLAB/OSIRIS/R (): A box model implementation of an AEM for linear waters with a focus on competition between various growth forms of macrophytes and the transfer of phosphorus, nitrogen and carbon through the food web. (http://en.wikipedia.org/wiki/PCDitch). (Van Liere et al. 2007).

PCDitch in DUFLOW (): A network implementation of an AEM for linear water structures with a focus on competition between various growth forms of macrophytes and the transfer of phosphorus, nitrogen and carbon through the food web. (http://en.wikipedia.org/wiki/PCDitch Van Liere et al. 2007).

PCDitch metamodel (): A metamodel of the outcomes of the box model implementation of PCDitch for a range of management relevant settings of the model. (Van Liere et al. 2007).

PCLake in ACSL/GRIND for MATLAB/OSIRIS/R (): A box model implementation of an AEM for linear waters with a focus on trophic interactions in the aquatic food web and transfer of phosphorus, nitrogen and carbon through the food web. (http://en.wikipedia.org/wiki/PCLake Janse et al. 2008, 2010).

PCLake in DELWAQ (): A 2D horizontal model implementation of an AEM for linear waters with a focus on trophic interactions in the aquatic food web and transfer of phosphorus, nitrogen and carbon through the food web. (http://en.wikipedia.org/wiki/PCLake Janse et al. 2008, 2010).
Text Box 1 continued

PCLake in DUFLOW (): A network implementation of an AEM for linear waters with a focus on trophic interactions in the aquatic food web and transfer of phosphorus, nitrogen and carbon through the food web. (http://en.wikipedia.org/wiki/PCLake | Janse et al. 2008, 2010).

PCLake in FABM (): A 1D vertical implementation of an AEM for linear waters with a focus on trophic interactions in the aquatic food web and transfer of phosphorus, nitrogen and carbon through the food web. (http://en.wikipedia.org/wiki/PCLake | Janse et al. 2008, 2010).

PCLake metamodel (): A metamodel of the outcomes of the box model implementation of PCLake for a range of management relevant settings of the model. (http://en.wikipedia.org/wiki/PCLake | http://themasites.pbl.nl/modellen/pclake | Janse et al. 2008, 2010).

PCLake submersed macrophyte equations (): A sub-model containing PCLAKE submersed macrophyte equations for stratified lakes that can be coupled to SALMO and GOTM in R. (http://r-forge.r-project.org/projects/rlimnolab, http://rlimnolab.r-forge.r-project.org | Sachse et al. 2014).

PCRGLOBWB (PCRaster Global Water Balance): A large-scale hydrological model intended for global to regional studies. (http://pcraster.geo.uu.nl/projects/applications/pcrglobwb | Van Beek et al. 2011; Sutanudjaja et al. 2014).

PDE (Partial differential equations): A function or a set of functions of multiple independent variables and its derivatives, in contrast to ODE. (http://en.wikipedia.org/wiki/Partial_differential_equation |).

PELETS-2D (Program for the Evaluation of Lagrangian Ensemble Transport Simulations): A program for the evaluation of Lagrangian ensemble transport simulations. (http://www.coastdat.de/applications/pelets_2d | Callies et al. 2011; Neumann et al. 2014).

Performance criteria (): A level of acceptable agreement between model and reality. The performance criteria apply both for model calibration and model validation. (Refsgaard and Henriksen 2004).

PERSIST (Pan-European Runoff Simulator for Solute Transport): A semi-distributed rainfall-runoff modelling toolkit for use with the INCA family of models. (http://www.slu.se/en/collaborative-centres-and-projects/slu-water-hub/models/persist, http://www.hydrol-earth-syst-sci.net/18/855/2014/hess-18-855-2014.html |).

PEST (model independent Parameter Estimation & Uncertainty Analysis): A standard software package for parameter estimation and uncertainty analysis of complex computer models. (http://www.pesthomepage.org | Doherty 2015).

PHOSMOD (PHOspHate MODel): A model to simulate the effects of fertilizers on plant growth and plant P concentration. (Greenwood et al. 2001).

PHREEQC (PH REdox EQuilibrium in C): A computer program for speciation, batch-reaction, one-dimensional transport, and inverse geochemical calculations. (http://wwwbrr.cr.usgs.gov/projects/GWC_coupled/phreeqc | Appelo and Postma 2005).

Physiologically structured population models (): An individual-based model approach in which growth, reproduction, mortality and interactions with other organisms are linked with individual traits in general and with size in particular. (De Roos and Persson 2001).

Piscator (): An individual-based model of fish communities. (http://www.projectenaew.wur.nl/piscator | Van Nes et al. 2002a).

Polar coordinates (): A two-dimensional coordinate system in which each point on a plane is determined by a distance from a reference point and an angle from a reference direction. (http://en.wikipedia.org/wiki/Polar_coordinate_system |).

POM (Pattern-Oriented Modelling): A bottom-up approach to the analysis of complex systems through a focus on only the relevant patterns in the real system, instead of trying to approximate the real system as closely as possible in all aspects. (http://en.wikipedia.org/wiki/Pattern-oriented_modeling | Grimm et al. 2005).

POM (Princeton Ocean Model): A 3D finite-difference open-source hydrodynamic model. (http://en.wikipedia.org/wiki/Princeton_ocean_model | http://www.ccpo.odu.edu/POMWEB, http://www.aos.princeton.edu/WWWPUBLIC/PROFS/NewPOMPage.html |).

Procedural programming (): A programming paradigm, derived from structured programming, based upon the concept of the procedure call to routines, subroutines, methods, or functions. (http://en.wikipedia.org/wiki/Procedural_programming |).

Process-based model (): A model that models the dynamics of the states of the system on the basis of the processes acting on these states. (http://www.coastalwiki.org/wiki/Process-based_modelling |).

PROTECH (Phytoplankton RosPSones To Environmental Change): A phytoplankton community model. (http://www.ceh.ac.uk/services/lake-ecosystem-models-assessing-phytoplankton | Reynolds et al. 2001; Elliott et al. 2010).

Python (): A general-purpose object-oriented high-level programming language. (http://en.wikipedia.org/wiki/Python_programming_language |).

QUAL2E (stream water QUALity Model, 2nd Enhanced version): A river and stream water quality model for 1D diurnal dynamics. (Brown and Barnwell 1987).
QUAL2 K (stream water QUALity Model): A river and stream water quality model for 1D diurnal dynamics. Updated version of QUAL2E. (http://www.epa.gov/athens/wwqtsc/html/qual2k.html | Chapra et al. 2008).

QUAL2 KW (stream water QUALity Model): A river and stream water quality model that is intended to represent a modernized version of the QUAL2E model and includes more processes than QUAL2K. (http://www.ecy.wa.gov/programs/eap/models.html | Pelletier et al. 2006).

R (programming language): A programming language and software environment for statistical computing and graphics. The package R/deSolve allows for numerical simulation of systems of differential equations. (http://en.wikipedia.org/wiki/R_(programming_language) | http://www.r-project.org, http://desolve.r-forge.r-project.org |).

Reality (natural system): A natural system that is the object of a particular scientific study. (http://en.wikipedia.org/wiki/Reality | | Refsgaard and Henriksen 2004).

Rectilinear grid: A n-dimensional grid consisting of rectangles. (http://en.wikipedia.org/wiki/Regular_grid | |).

Regime shift: A relatively abrupt change from one regime to a contrasting one, where a regime is a dynamic ‘state’ of a system with its characteristics stochastic fluctuations and/or cycles. (http://en.wikipedia.org/wiki/Regime_shift | | Scheffer et al. 2009).

Regression model: A statistical technique for estimating the relationship between a dependent variable and one or more independent variables. (http://en.wikipedia.org/wiki/Regression_analysis | |).

Regular grid: A n-dimensional grid of paralleloptopes such as rectangles, parallelograms or cuboids. (http://en.wikipedia.org/wiki/Regular_grid | |).

RIVERSTRAHLER: A nutrient and phytoplankton model for rivers. (Billen et al. 1994).

RIVPACS (River InVertebrate Prediction And Classification System): A statistical model relating species composition in rivers to abiotic factors. (http://www.ceh.ac.uk/products/software/rivpacs.html |).

ROMS (Regional Ocean Modeling System): A free-surface, terrain-following, primitive equations ocean model. (http://en.wikipedia.org/wiki/Regional_Ocean_Modeling_System | https://www.myroms.org | Shchepetkin and McWilliams 2005).

ROMS-BGC (Regional Ocean Modeling System BioGeoChemical model): An ocean biogeochemical model with various configuration options. (http://www.myroms.org | Xiao and Friedrichs 2014).

rSALMO (Simulation by an Analytical Lake MOdel): A dynamic ecological model that simulates main compartments of the pelagic food web of lakes and reservoirs implemented in R. It can link to a sub-model for PCLake’s submerged macrophytes and can be driven by hydrophysics provided by external models. 0D to 1D model grids can be set up. (https://r-forge.r-project.org/projects/rimmolab |).

Runge–Kutta integration: An important family of implicit and explicit iterative methods to numerically solve ordinary differential equations. (http://en.wikipedia.org/wiki/Runge%E2%80%93Kutta_methods | |).

Runoff model: A mathematical model describing the rainfall–runoff relations of a rainfall catchment area, drainage basin or watershed. (http://en.wikipedia.org/wiki/Runoff_model_(reservoir) | |).

SALMO 1D/HR (Simulation by an Analytical Lake MOdel): A dynamic ecological model that simulates main compartments of the pelagic food web of lakes and reservoirs implemented in Delphi and C. (http://www.simecol.de/salmo | Benndorf and Recknagel 1982; Baumert et al. 2005).

SALMO 2 (Simulation by an Analytical Lake MOdel): A dynamic ecological model that simulates main compartments of the pelagic food web of lakes and reservoirs implemented in Java. (http://www.simecol.de/salmo | Benndorf and Recknagel 1982; Petzoldt and Siemens 2002).

Scenario analysis: A process of analysing possible future events by considering alternative possible outcomes. In contrast to prognoses, scenario analysis does not aim at extrapolation of the past. Instead, it tries to consider a whole suite of possible developments and turning points for the future. (http://en.wikipedia.org/wiki/Scenario_analysis | |).

SCOBI (Swedish Coastal and Ocean BIogeochemical model): A functional-group-based phytoplankton and water quality model. (http://www.smhi.se/en/research/research-departments/oceanography/scobi-1.8680 | Eilola et al. 2009).

Scripting language: A programming language that supports interpreted—rather than compiled—scripts that automate the execution of tasks that could alternatively be executed one by one by a human operator. (http://en.wikipedia.org/wiki/Scripting_language | |).

SENCEA (Simulation ENVironment for ECological Application): A modelling framework for the implementation of AEMs. (De Hoop et al. 1992).

Sensitivity analysis: A quantification of the change in model output as a function of the change in model input. (http://en.wikipedia.org/wiki/Sensitivity_analysis | |).
Text Box 1 continued

SHOC (Sparse Hydrodynamic Ocean Code): A sparse coordinate hydrodynamic model optimized for coastal systems. (l http://www.emg.cmar.csiro.au/www/en/emg/software/EMS/hydrodynamics.html l Wild-Allen et al. 2010; Oke et al. 2013; Herzfeld and Waring 2014).

SIMCAT (SIMulation of CATchments): A very simple water quality model for lakes. (l l Comber et al. 2013).

SIMSTRAT (): A 1D-model for simulating mixing, stratification and temperature in lakes, based on k-epsilon approach, including the effects of internal waves. (l l Goudsmit et al. 2002).

Simulation (): (l l See Temporal simulation).

SMART (Simulation and Modelling Assistance for Research and Training): A tutorial modelling framework for the implementation of dynamical models that is structured in database fashion and therefore bears resemblance with DATM. Next to implementation SMART enables running of models in a structured way, i.e. in model experiments, that contain the model version and input used and the resulting output. (l http://harmoniqua.wur.nl/smart l Kramer and Scholten 2001).

SOBEK (after SOBEK, the ancient Egyptian god of the nile): A 1D/2D modelling suite for flood forecasting, optimization of drainage systems, control of irrigation systems, sewer overflow design, river morphology, salt intrusion and surface water quality. (l http://www.deltares.nl/en/software/sobek l).

Software application (): A set of user-written code within a modelling framework that is designed to execute certain functions or tasks. (l l).

Software framework (): - (l l See Modelling framework).

Software library (): A set of functions or routines that can be called from a software application to perform a specific task, e.g. numerical integration. (http://en.wikipedia.org/wiki/Library_(computing) l l).

Spatially explicit model (): A model that explicitly takes space into account. This can be done with vector- or grid-based approaches. (l l Minor et al. 2008).

SPM in FABM (Suspected Particulate Matter model): A suspended particulate matter pelagic model with multiple size classes. (l http://sf.net/p/fabm l Burchard et al. 2004).

Statistical model (): A set of assumptions concerning the generation of the observed data and similar data from a larger population. (http://en.wikipedia.org/wiki/Statistical_model l l).

STELLA (): A modelling framework that allows for drag-and-drop modelling in a graphical user interface. (l http://www.iseesystems.com/softwares/Education/StellaSoftware.aspx l).

Stoichiometric model (): A modelling approach that considers how the balance of energy and elements affects and is affected by organisms and their interactions in ecosystems. (http://en.wikipedia.org/wiki/Ecological_stoichiometry l l).

Structural equation model (): A statistical model based on the combination of two components: a measurement model that defines latent variables using one or more observed variables, and a structural regression model that links latent variables together. (http://en.wikipedia.org/wiki/Structural_equationModeling l l).

Structural uncertainty (): A misestimate of the data by the model’s output due to missing or imperfect process formulations within the model. (http://en.wikipedia.org/wiki/Uncertainty_quantification l l).

Structured grid (): (l l See Curvilinear grid).

SWAN (Simulating WAves Nearshore): A wave model for wind-generated waves in coastal regions and inland waters. (l http://www.swan.tudelft.nl, http://swanmodel.sourceforge.net l Booij et al. 1996).

SWAT (Soil and Water Assessment Tool): A semi-distribution eco-hydrological model. (http://en.wikipedia.org/wiki/SWAT_model l http://swat.tamu.edu l Arnold et al. 1998).

SWATCUP (Soil and Water Assessment Tool Calibration and Uncertainty Procedure): A calibration utility for the SWAT model. (http://en.wikipedia.org/wiki/Swat-CUP l l Abbaspour 2007; Abbaspour et al. 2007).

SWMM (Storm Water Management Model): A dynamic rainfall–runoff–subsurface runoff simulation model primarily for urban and suburban areas. (http://en.wikipedia.org/wiki/Storm_Water_Management_Model l l).

TDT (Typed Data Transfer library): An interface for the transmission of data between programs in a platform- and programming language-independent way. (l https://www.pik-potsdam.de/research/transdisciplinary-concepts-and-methods/ archive/projects/modsimenv/modenv/tdt l).

Telemac (): An integrated suite of solvers for use in the field of free-surface flow. (http://en.wikipedia.org/wiki/TELEMAC l http://www.opentelemac.org l).

Temporal simulation (): A basic model analysis technique in which time series of output data are produced, mostly by numerical integration of process formulations in the form of ordinary, partial, or lattice differential equations. (http://en.wikipedia.org/wiki/Computer_simulation l l Refsgaard and Henriksen 2004).
Text Box 1 continued

Trait-based model (): An individual-based model approach in which growth, reproduction, mortality and interactions with other organisms are linked with individual traits. (http://bio.uib.no/te/research/traits.php).

Triangular mesh (): A mesh grid consisting of triangles in one, two or three dimensions. (http://en.wikipedia.org/wiki/Triangle_mesh).

TRIM (Tidal, Residual and Inter-tidal Mutflat model): A hydrodynamic model optimized for coastal systems. (http://sfbay.wr.usgs.gov/watershed/hydro_model.html | Cheng et al. 1993; Cugier and Le Hir 2002).

TUFLOW-FV (Two-dimensional Unsteady FLOW Finite-Volume): A 3D flexible mesh finite volume hydrodynamic model. (http://www.tuflow.com/Tuflow%20FV.aspx | Jamieson et al. 2012; Bruce et al. 2014).

Uncertainty analysis (): A quantification of the uncertainty in model output as a function of the uncertainty in model input. (http://en.wikipedia.org/wiki/Uncertainty_analysis).

Validation (): (See Model validation).

VisSim (VISual language for SIMulating nonlinear dynamic systems): A visual block diagram language for simulation nonlinear dynamic systems. (http://en.wikipedia.org/wiki/VisSim | http://www.vissim.com).

Visual Basic (): An object-oriented programming language and integrated development environment. (http://en.wikipedia.org/wiki/Visual_basic | https://msdn.microsoft.com/en-us/vstudio/ms788229.aspx).

Vollenweider model (): An empirical and statistical lake eutrophication. (http://en.wikipedia.org/wiki/Richard_Vollenweider | Vollenweider 1975).

WAFLEX (): A spreadsheet-based model. It can be used to analyse upstream–downstream interactions, dam management options and water allocation and development options. (http://en.wikipedia.org/wiki/WAFLEX).

WASP (Water quality Analysis Simulation model): A dynamic water quality model used to investigate pollutants in aquatic systems in 1D, 2D, and 3D. (http://www.epa.gov/athens/wwqtec/html/wasp.html).

Water Framework Explorer (): An analysis tool to calculate the effect of restoration and mitigation measures on the ecological and chemical quality of surface waters. (https://www.deltares.nl/en/projects/water-framework-directive-explorer, https://publicwiki.deltares.nl/display/KRWV/KRW-Verkenner).

Water quality model (): A formal procedure by which the impact of external or internal forcing on water quality parameters can be estimated. Water quality model is sometimes used as a synonym for AEM. (http://en.wikipedia.org/wiki/Water_quality_modelling).

Water quantity model (): (See Hydraulic model, Hydrodynamic model and Hydrological model).

WATERRAT (WATER quality Risk Analysis Tool): A spreadsheet-based modelling package used to make decisions in the management of surface water quality. (McIntyre et al. 2003; McIntyre and Wheater 2004).

WMS (Watershed Modeling System): A model for water quantity and quality in watersheds. (http://en.wikipedia.org/wiki/WMS (hydrology_software) | http://www.xmswiki.com/wiki/WMS:WMS).

WWQM (Wetlands Water Quality Model): A model of constructed wetland dynamics. (Chavan and Dennett 2008; Huang et al. 2014).

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