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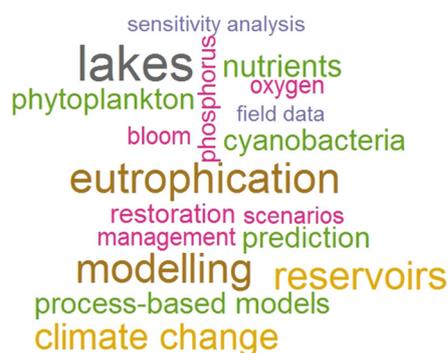
Modelling eutrophication in lake ecosystems: A review

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HIGHLIGHTS

- Lake eutrophication models applied to study sites with management objectives
- Focus on process-based models and cyanobacteria dynamics
- Coupling of hydrodynamics and ecological processes
- Comparison of model results to field data
- Review based on a validated methodology of Scientific Collective Expertise

GRAPHICAL ABSTRACT



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ABSTRACT

Eutrophication is one of the main causes of the degradation of lake ecosystems. Its intensification during the last decades has led the stakeholders to seek for water management and restoration solutions, including those based on modelling approaches. This paper presents a review of lake eutrophication modelling, on the basis of a scientific appraisal performed by researchers for the French ministries of Environment and Agriculture. After a brief introduction presenting the scientific context, a bibliography analysis is presented. Then the main results obtained with process-based models are summarized. A synthesis of the scientist recommendations in order to improve the lake eutrophication modelling is finally given before the conclusion.

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1. Introduction

Eutrophication of aquatic ecosystems refers to an ecological state, where biological processes driven by increased nutrient loading from their watershed conduct to proliferation of primary producers (phytoplankton, aquatic plants, cyanobacteria), hypoxia or even anoxia and loss of biodiversity. Worldwide, eutrophication is one of the main causes

of the degradation of the ecological state in inland and coastal waters. Eutrophication has been observed since the beginning of the twentieth century in industrialized countries (e.g. Le Moal et al., 2018; Moss, 2012; Takolander et al., 2017; Yao et al., 2018). However, during the last decade, eutrophication has become a more pregnant societal issue, encompassing many different stakes, from ecological to economic and political, which must be tackled at the scale of the concerned territories by the involved stakeholders.

Lakes and reservoirs are part of the hydrological cycle of their watershed. Fluxes are permanently exchanged between the lake and the

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atmosphere, the ground and surface waters. Lakes play an essential role in the biogeochemical cycles of continental watersheds. Two processes drive these biogeochemical cycles, particularly carbon, nitrogen and phosphorus cycles: the primary production and the settling of particulate matter.

In lakes, the current velocities are generally low and the water residence time high. Therefore, lakes provide us with a time-integrated response to the external forcing. The analysis of their time trajectory can allow us to better understand the biological and physical, local and global pressures that they face (Perga et al., 2016; Schindler, 2009).

Lake ecosystems are particularly sensitive to nutrient loading from their catchment because of the thermal stratification of the water column during the period when the primary production is maximal (spring and summer). The thermal stratification divides the water column into two layers: the upper layer, the warmer and lighted epilimnion, where primary production occurs, and a colder deeper layer, the hypolimnion. Thermal stratification occurs in all lakes but extending on different time scales. In shallow lakes, thermal stratification hardly lasts more than a few hours or days. The main morphometric (depth, volume) and hydrological (discharge of the tributaries, surface and land-use in the catchment) characteristics will determine the lake vulnerability to eutrophication.

In the early 1960s, lakes were the first water bodies where eutrophication effects were observed, mainly on the water resources used for drinking water supply (e.g. Dillon and Rigler, 1974a; Vollenweider and Kerekes, 1982). Actually, lake eutrophication started in industrialized countries since the 1930s as it is indicated by recent outcomes based on paleo-limnological studies. This is the case in Europe, for example for Lake Bourget (France) where eutrophication appeared around 1933 (Giguet-Covex et al., 2010; Jenny et al., 2013).

In the 1960–1980s, lake eutrophication was widely described, in particular in symposia devoted to this topic like the Madison Symposium (National Academy of Sciences, 1969) or the Symposium of the American Society of Limnology and Oceanography (ASLO) in 1971. Historically, the description of lake eutrophication was more directed to deep lakes, located in the Northern hemisphere (United States, Canada, and Western Europe) and Australia. The general acceptance of lake trophic state classification, “oligotrophic”, “mesotrophic” and “eutrophic” follows the studies of the Organisation for Economic Co-operation and Development (OECD) in the late 1970s (Vollenweider, 1975; Vollenweider and Kerekes, 1982).

The main effects of lake eutrophication are an increase of phytoplankton biomass, where cyanobacteria frequently dominate, a decrease of water transparency and a clear difference between surface layers, rich in oxygen, and the deoxygenated hypolimnion (Dodds, 2006; Wetzel, 2001). Hypoxia in the hypolimnion leads to an internal phosphorus load released by the sediment, which in turn amplifies the eutrophication of the system (Dodds, 2006).

Eutrophication has been one of the main threats for water quality in lakes and reservoirs since the 1960s. In spite of number of research works conducted during the last five decades, eutrophication remains a major concern worldwide (Smith et al., 2006). More than 40% of lakes are eutrophic and affected by algal blooms (Bartram et al., 1999). The issues to be addressed still regard interactions between nutrients, principally phosphorus which is generally the main cause of lake eutrophication, and the ecological functioning. New manifestations of eutrophication have emerged during the last two decades (Anderson et al., 2012; Le Moal et al., 2018; Pomati et al., 2017). Among the phytoplankton species, cyanobacteria have gained an increased interest, due to the worldwide occurrence of their blooms. The increasing frequency of cyanobacteria blooms might be linked to climate change.

The management and restoration solutions to control eutrophication must be supported by scientific outcomes, including modelling approaches. Since the 1970s and the awareness of the negative impact of eutrophication on lake ecosystems, numerical modelling was considered as an interesting tool (Imboden, 1974; Vollenweider, 1975;

Vollenweider and Kerekes, 1982). Many models were developed, often to obtain predictive tools used as support for lake management and to define targets of nutrient loading reduction by the catchment. The model key state variables are those that link primary production to nutrients, principally phosphorus, nitrogen and sometimes silica (De Senerpont Domis et al., 2014; Reynolds et al., 2001). Cyanobacteria growth also raises new modelling issues to represent processes such as nitrogen fixation, uptake of nutrient organic forms and mobility of the cells.

In order to support public decision-making, issues raised by public entities, for example a ministry, can be addressed in the form of a multidisciplinary critical assessment of available scientific knowledge, called collective scientific expertise. In 2016, two French ministries respectively in charge of Environment and Agriculture, initiated a collective scientific expertise (Expertise Scientifique Collective, ESCo in French), bringing together scientific knowledge available on the eutrophication issue (Pinay et al., 2017). The objective was to improve the consistency and effectiveness of public action on eutrophication control. One chapter of the scientific expertise report was devoted to eutrophication modelling (Crave et al., 2017). This chapter included five sections respectively entitled “Modelling of non-point nutrient loading in the catchment”, “Modelling in-stream processes”, “A focus on sediment transport modelling”, “Modelling eutrophication in coastal ecosystems” and “Modelling eutrophication in lake ecosystems”. A review of marine eutrophication models derived from this scientific expertise study can be found in (Mènesguen and Lacroix, 2018). The paper presented hereafter is based on the chapter focusing on lake eutrophication modelling and including a large review of modelling studies.

The bibliographic corpus that we considered is composed of 438 references obtained by using the bibliographic search tool proposed by Web of Science (see Appendix A.1 for details). The paper is organized as follows. In Section 2, the bibliographic corpus is analysed according to the following items: study sites, objectives, model typology and main research topics. Additional statistics about the number of publications and citations; the general categories, research areas and journal titles; and the keywords of the references included in the bibliographic corpus are given in Appendix A. Section 3 is dedicated to the modelling results obtained with process-based models. Finally we summarize the scientist recommendations in order to improve the lake eutrophication modelling in Section 4, and we raise some key issues for future achievements in this research field in the conclusion section.

2. Bibliography analysis

2.1. Study sites

Several lakes have been considered as case studies for the application of eutrophication models. An automatic search routine was implemented to search for the names of lakes in the title, abstract and keywords of the references of the bibliographic corpus. It led to a list of 118 lake names and 230 references. The repartition of the references according to the continent, the country and the name of the lakes is given in Table 1. The evolution over the time of the number of publications according to the continent of the studied lake is given in Fig. 1.

The most studied lakes are located in North America (mostly in the USA and Canada) and Asia (in China, Japan, Turkey and Russia). Lakes of Western Europe (in The Netherlands, Estonia, Switzerland and Germany) and Northern Europe (in Finland and the United Kingdom) also received special attention. The Great lakes or Laurentian lakes (Lakes Erie, Ontario, Michigan, Superior and Huron) located between the USA and Canada are the subject of numerous publications. Apart from them, we can mention the particular case of Lake Taihu (China) that is intensively studied (26 papers), as much as for Lake Erie but at a different pace. Publications on Lake Erie started in 1984 and on Lake Taihu in 2004. Among the other lakes, there are many large lakes with a surface area over 100 km², as it is the case of Lake Dianchi (China),

Table 1

Number of publications depending on the continent, the country and the name of the studied lake. Only the countries and the lakes that have been found in three or more than three publications are listed.

Continent	Number of publications	Country	Number of publications	Lake name	Area (km ²)	Number of publications
North America	94	USA-Canada	62	Great lakes	244,000	47
Asia	75	China	51	Lake Erie	25,700	27
Western Europe	20	USA	39	Lake Taihu	2250	26
Northern Europe	19	Netherlands	10	Lake Ontario	19,000	13
Eastern Europe	7	Japan	8	Lake Michigan	58,000	11
Southern Europe	6	Finland	7	Lake Superior	82,000	9
Oceania	6	Canada	7	Lake Dianchi	298	9
Southern Europe	5	Israel	6	Lake Washington	88	8
Africa	5	United Kingdom	5	Lake Huron	60,000	6
		Hungary	5	Lake Kinneret	166	6
		New-Zealand	4	Lake Balaton	592	5
		Estonia-Russia	3	Lake Veluwe	30	5
		Greece	3	Lake Chaohu	760	5
		Switzerland	3	Lake Okeechobee	1891	4
		Germany	3	Lake Peipsi	3555	3
		Turkey	3	Lake Bassenthwaite	5	3
		Russia	3	Lake Columbia	3	3
				Lake Spokane	19	3
				Lake Kasumigaura	220	3

Kinneret (Israel), Balaton (Hungary), Chaohu (China), Okeechobee (USA), Peipsi (Finland) and Kasumigaura (Japan).

Regarding the time evolution, the lakes that were studied during the 1970s and the 1980s are mainly located in North America (Ditoro et al., 1987; Snodgrass, 1987, 1985). In the 1990s, modelling works were then carried out on lakes from Western Europe (Asaeda and Van Bon, 1997; Hollander et al., 1993). And since 2000, there has been a significant increase in modelling studies conducted on Chinese lakes, particularly since 2010 (Hou et al., 2004; Huang et al., 2012; W. Li et al., 2014). In parallel, lake ecosystems from South America (Fragoso et al., 2008), Southern Europe (Alonso Fernandez et al., 2014), Middle East such as Karaoun reservoir in Lebanon (Fadel et al., 2017) but mainly Lake Kinneret in Israel (Bruce et al., 2006; Gal et al., 2009) and Africa (Asaeda et al., 2001) were also modelled.

Finally, models have also been applied to high-altitude or high-latitude lakes in recent years (Patynen et al., 2014; Romshoo and Muslim, 2011). Similarly, the preservation of ecological continuity in the urban and peri-urban environment and the promotion of Nature-based solutions for the urban water management led to recent modelling works of small urban lakes (e.g. Gong et al., 2016; Soullignac et al., 2017).

2.2. Modelling objectives

Several purposes have led to the development of lake eutrophication models. Although eutrophication models are not only used for management purposes but also for research (Simonsen and Dahl-Madsen,

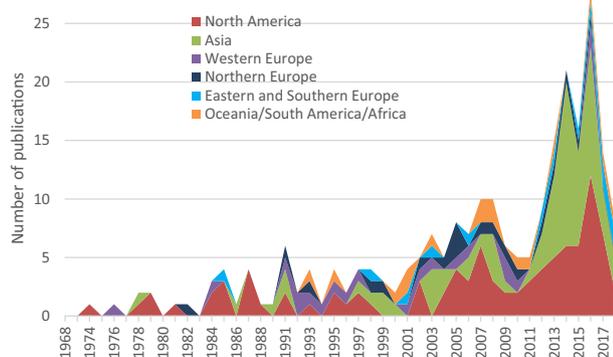


Fig. 1. Time evolution of the number of publications according to the continent of the studied lake.

1978; Vanhuet, 1992), we will focus in this paper mainly on the management objectives. In the keyword analysis, the words “management”, “simulation”, “prediction” and “restoration” appear respectively in 54, 49, 31 and 22 references of the bibliographic corpus, which represents 12%, 11%, 7% and 5% of the references. This shows how lake eutrophication is a concerning problem for which practical solutions are needed.

In the 1970s, the OECD model (Vollenweider, 1975), that has been calibrated on a data set coming from more than 200 lakes of several continents, was used to predict the eutrophication response to phosphorus loading. The nutrient load limits in the USA and Canada have been established from this model.

Some models have been used to assess the conditions for achieving regulatory or management objectives. For example, the 1D vertical model DYRESM-CAEDYM was used to compute the level of phosphorus input reduction necessary to make the ecological status of Lake Ravn (Denmark) comply with the requirements of the European Water Framework Directive (Trolle et al., 2008).

Models are also developed to perform numerical experiments. Recently, the sharp increase in the number of reservoirs worldwide (World Commission on Dams, 2000), for irrigation, drinking water production and hydroelectricity, has led researchers to investigate the effects of eutrophication on the carbon and greenhouse gas cycle in these water bodies (Chanudet et al., 2012; Stepanenko et al., 2016). Models are also used to predict the functioning and the impact of a reservoir that is expected to be built (Inkala et al., 1998). Conversely, some papers focus on the simulation of the impact of climate changes on lake eutrophication (Elliott and Defew, 2012; Hassan et al., 1998; Schwefel et al., 2016). It includes the increase of temperature (Markensten et al., 2010) and the intensification of extreme climatic events such as floods (Brito et al., 2017) or storms (Schwalb et al., 2015).

Model of lake eutrophication are also often used to predict the evolution of variables of interest. In the short term (one or two weeks), the objective can be to predict algal blooms, particularly cyanobacteria blooms. It makes it possible to anticipate the measures to be taken depending on the water body use: recreational activities such as bathing, production of drinking water, etc. (Huang et al., 2015, 2012; W. Li et al., 2014; Recknagel et al., 2016). Over longer time-scales, models are used to predict the response of lake ecosystems to climate change scenarios or local changes in nutrient input (Chapra and Canale, 1991; Pipp and Rott, 1995), sometimes with a special focus on cyanobacteria dynamics (Howard and Easthope, 2002; Markensten et al., 2010; Varis, 1993).

Finally, models are also developed to test some control strategies for the restoration of lakes (e.g. Sagehashi et al., 2001). The reduction of

nutrient loads is the most studied strategy (e.g. Lindim et al., 2015; Ozkundakci et al., 2011). Some papers focus on biomanipulation which consists in adding or removing species from the ecosystem (Jayaweera and Asaeda, 1996; Ogilvie and Mitchell, 1995; Sagehashi et al., 2001). Other alternative lake restoration techniques are studied, such as sediment dredging (Sagehashi et al., 2001), water diversion (Liu et al., 2014), addition of macrophytes (Xu et al., 2014, 1999) or hypolimnetic oxygenation (Moore et al., 1996; Sahoo and Luketina, 2003; Singleton et al., 2010; Toffolon and Serafini, 2013).

2.3. Model typology

The scientific community early recognized the value of mathematical modelling for the study of lake ecosystems. Researchers have developed numerous models of various types. Recent reviews of lake modelling developments can be found in (Bhagowati and Ahamad, 2018; Jørgensen, 2010). Depending on how the ecosystem is represented mathematically, we can distinguish several classes of models (see for example Jørgensen and Fath, 2001; Mooij et al., 2010). Thus, models are generally first separated in two classes: empirical models and mechanistic models (Fornarelli et al., 2013).

2.3.1. Empirical models

Empirical models, also called data-oriented models (Afshar et al., 2012) or data-driven models (Elshorbagy and Ormsbee, 2006) are derived from the available data sets. They mainly consist in statistical relationships (called transfer functions) between predictor variables and response variables of interest. The first empirical models that were developed were regression models that assume linear relationships between the variables as it is the case for the nutrient-chlorophyll relationships given in (Dillon and Rigler, 1974a; Reckhow, 1993). Empirical models present several advantages: they require little *a priori* knowledge about the ecosystem processes and the data themselves; few data and “simple mathematics are needed” and these models are generic and “give good predictions for a group of lakes” (Vanhuét, 1992). However, when applied to an individual lake, empirical models often lead to large uncertainties. According to Vanhuét (1992), “empirical models are often applied if only mean annually values are of interest”. However, due to the rapid progress in available computational power, and to the increasing use of high frequency measurement systems based on *in situ* sensors, interest in empirical models is still growing. These models are used for different purposes, for example to re-analyse statistical relationships between nutrients and chlorophyll in different contexts (Brown et al., 2000; Huszar et al., 2006). New statistical approaches are also proposed to improve the quality of the models. For example, quantile regression is applied instead of ordinary least square regression in (Xu et al., 2015a, 2015b) and a Bayesian approach is used to link nutrient and chlorophyll concentrations in (Freeman et al., 2009). Bayesian model averaging has also been proposed to predict the occurrence of harmful algal blooms (Hamilton et al., 2009). However, these models provide results associated with a very large level of uncertainty and over time scales too long to study the short-term response to a decrease in nutrient inputs by the watershed; they therefore lack precision to be used by managers (Reynolds and Elliott, 2010).

Statistical models of the 1970s and 1980s have evolved significantly over the last decade towards “data-driven” models. Such models need large data sets that were not available in the past, but that lake monitoring systems are now able to collect. Artificial neural networks (ANNs) are now commonly used to study lake eutrophication (Chen and Liu, 2014; leong et al., 2015; Millie et al., 2006; Rankovic et al., 2010), because of “their recognized capability in predicting highly nonlinear and complex relationships” (Fornarelli et al., 2013). However, if ANNs provide interesting prediction tools, their construction is a “highly demanding task, particularly when dealing with short and noisy ecological data” (Chaves and Kojiri, 2007; Fornarelli et al., 2013; Kim et al., 2012).

Other data-driven models using machine learning techniques such as tree-based models (Fornarelli et al., 2013; Jung et al., 2010; Peretyatko et al., 2012), support vector machines (Diaz Muniz et al., 2015; Garcia-Nieto et al., 2018; Xu et al., 2015a, 2015b) or random forests (Hallstan et al., 2012) are also proposed. For short-term (day to weeks) forecast, such data-driven models give good results, but for the simulation of long-term prospective scenarios, they hardly can be used as it is necessary to include knowledge about the driving processes.

2.3.2. Mechanistic models

Mechanistic models, also called process-oriented models (Arhonditsis and Brett, 2004), process-based models (Fornarelli et al., 2013) or theoretical models (Vanhuét, 1992), are based on the *a priori* knowledge of the driving processes of the ecosystem. Most of them consist in a set of differential or difference equations which describe in details the biogeochemical processes and whose solution is obtained by numerical methods. Several review papers focusing on mechanistic models have been published (e.g. Anagnostou et al., 2017; Arhonditsis and Brett, 2004).

In the 1980s, mechanistic models generally computed the steady-state concentration of variables, leading to nonlinear static relationships between variables of interest (e.g. Imboden, 1974; Schnoor and O'Connor, 1980; Vollenweider, 1975). These models are called “input-output” models (Vollenweider, 1975) or black-box models (Teruggi and Vendegna, 1986) and are sometimes considered as empirical models whereas their structure is directly deduced from dynamic equations of biogeochemical processes. The data that generally come from a group of lakes, are only used to identify the model parameters with statistical methods. This approach has been widely used to estimate the trophic state of numerous lakes (e.g. Jones and Bachmann, 1976; Dillon and Rigler, 1974b). As they are based on a steady-state assumption, input-output models fail to “predict the dynamic trend of eutrophication in a large reservoir with temporal variation in inflow and storage” (Afshar et al., 2012). Moreover, these models “do not describe the biological variables which are of main interest” and “do not take into account the influence of biological processes on the model parameters” and some “important interactions between several phytoplankton limiting factors, light, phosphorus, nitrogen” (Simonsen and Dahl-Madsen, 1978).

Most mechanistic models are dynamic. Mooij et al. (2010) make the distinction between “minimal dynamic models”, “complex dynamic models” and “structurally dynamic model”. Minimal dynamic models are simple and composed of only a few differential or differences equations; they “often generate a hypothesis about a possible cause of a phenomenon that would not easily be arrived at intuitively” (Mooij et al., 2010). On the contrary, complex dynamic models (e.g. CAEDYM, PCLake, DELWAQ) include numerous variables and processes and are designed to be used as a virtual reality for the simulation of the whole ecosystem. They are therefore often coupled with a detailed hydrodynamic model and validated on field data. A comparison between nine complex dynamic models commonly used to study eutrophication can be found in (Anagnostou et al., 2017). Structurally dynamic models have then been proposed to add flexibility in the structure of the models (Jørgensen, 2015). The idea is to make the model parameters vary over time, based on the expert knowledge or by optimization of a well-chosen goal function. Kalman filter (Huang et al., 2013) is based on similar idea: by addition of a “correction” term in the equations of the model, it enables to adjust the model variables depending on the measurements. Finally, we can mention the particular case of the BLOOM model (Los, 1980) which also relies on optimization techniques: it is based on the computation of the optimal species composition *via* linear programming.

In the above-mentioned models, the ecosystem is described at the population level. The need to take into account some specific features of the populations, such as size distribution or other traits, led the researchers to use the individual-based approach (DeAngelis and Mooij,

2005). As it is “too computationally demanding to model all individuals separately” (Mooij et al., 2010), derived approaches that are computationally more efficient, have been proposed, such as super-individual models, physiologically structured population models, stage-structured biomass models, and trait-based models. Mention should be made of other approaches such as energy system language (e.g. Rivera et al., 2007).

Mechanistic models have been applied to many lakes (e.g. Cui et al., 2016; Hou et al., 2004; Takkouk and Casamitjana, 2016), and their contribution to the study of the spatio-temporal dynamics of ecosystems is widely recognized. In particular, hydrodynamic processes are represented accurately. However with regard to biological processes, because of the complexity of the process interplay, and the lack of knowledge, mechanistic models still need to be improved. Mechanistic models are already complex and involve a large set of parameters (sometimes more than 100) to be calibrated. As a consequence, the outcomes of simulated scenarios are hampered with great uncertainty (Gal et al., 2014). The calibration itself is a difficult task because it necessitates the use of extensive data sets (Elshorbagy and Ormsbee, 2006) and because the simulations, particularly when coupled with 3D hydrodynamic models, are computationally demanding. Limitations concerning their application at the decision-making level have been emphasized (Fornarelli et al., 2013). Nevertheless, deterministic models remain best suited to simulate the spatio-temporal response of lake ecosystems to forcing change scenarios. Moreover the increase of the computational power should facilitate the use of such models in the future.

Note that mechanistic models are often deterministic but the stochastic nature of the events and pathways leading to eutrophication should encourage the use of stochastic components (Kutas and Toth, 1985; Sarkar and Chattopadhyay, 2003; Wang and Qi, 2018).

2.3.3. From box models to 3D models

To reproduce accurately the ecosystem dynamics, mechanistic models are frequently coupled with a hydrodynamic model that can be quite simple, simulating only the water temperature and the regime of temperature stratification and mixing or more complex, simulating also the current velocities and patterns.

The spatial dimension of the coupled models varies from zero (box models): in that case “the water body of a lake or of each box within a lake is represented as a completely mixed stirred tank reactor” (Nyholm, 1978), to three: the spatial heterogeneity of the ecosystem is taken into account in all three dimensions. If a box model alone cannot account for the lake spatial heterogeneity, this can be obtained using a set of interconnected box models (Muraoka and Fukushima, 1986; Nyholm, 1978). For example, Smiths lake has been divided into 11 boxes, each of them is represented as a well-mixed reactor, connected to its neighbouring boxes through fluxes (Everett et al., 2007). For the vertical dimension, some models simulate the thermal stratification by using 2-box models with one box for the epilimnion and one box for the hypolimnion (Frisk, 1982; Imboden, 1974; Imboden and Gächter, 1978; Rodriguez Reartes et al., 2016).

Vertical 1D models are also frequently used to simulate the thermal stratification and its influence on phytoplankton, nutrient and oxygen dynamics (Bell et al., 2006; Fennel et al., 2007; Trolle et al., 2008). 2D models, more rarely used, are developed for large but shallow systems where thermal stratification is negligible (Fragoso et al., 2008; Huang et al., 2012; Zhang et al., 2008). 3D models appeared in the early 2000s (Kuo and Thomann, 1983), but it was in the 2010s, due to the increase of computational power and of *in situ* measurements, that 3D models have been increasingly applied to lakes (Carraro et al., 2012; Deus et al., 2013; Leon et al., 2011; Schwalb et al., 2015; Soullignac et al., 2017).

The coupling of models can be a difficult task. The Framework for Aquatic Biogeochemical Models (FABM) has been developed to facilitate the coupling between several hydrodynamic models and ecological models (Trolle et al., 2011a).

2.4. Main research topics studied with lake models

As shown by the keywords analysis (see Appendix A.4), the models can represent different components of the ecosystem. In the following section, we will analyse more in details how these components are represented: (1) phytoplankton; (2) nutrients; (3) sediments; (4) oxygen; (5) cyanobacteria.

2.4.1. Phytoplankton

A significant number of references of the bibliographic corpus (115 references, 26% of the total) are marked with the keyword “phytoplankton” which shows the importance given to the modelling of phytoplankton dynamics (Elliott and Thackeray, 2004; Frisk et al., 1999; Hillmer et al., 2008; Reynolds and Irish, 1997; Rukhovets et al., 2003; Seip, 1991).

In many models, in particular empirical models but also water quality models, only the total phytoplankton biomass is represented. In recent years, the study of changes in phytoplankton community composition has received special attention, leading to the development of phytoplankton succession models (Rigosi et al., 2010). In these models, the phytoplankton community is divided into different groups, either by modelling all the species individually or by incorporating community information into the models (Hallstan et al., 2012). Generally, the phytoplankton modelling relies on a representation of the functional characteristics of species (Hallstan et al., 2012; Jones and Elliott, 2007; Kerimoglu et al., 2017; Mieleitner and Reichert, 2008, 2006). In a few cases, models seek to represent the functioning of individuals in a phytoplankton population during the different stages of their life cycle through the use of “agent-based” or “individual based models” (Hellweger et al., 2008). These models can be used to predict either short-term changes in phytoplankton community composition (Huang et al., 2014, 2012), or medium to long term changes (Elliott et al., 2005; Markensten et al., 2010). 3D models allow for better consideration of spatial heterogeneities in phytoplankton development (Hillmer et al., 2008; Leon et al., 2012, 2011).

Some studies focus on the modelling of particular processes, such as: (1) the influence of physical functioning on phytoplankton dynamics (Bernhardt et al., 2008; Elliott et al., 2009; Elliott and Defew, 2012; Gulliver and Stephan, 1982; Jones and Elliott, 2007; Na and Park, 2006; Patynen et al., 2014; Verhagen, 1994); (2) the relationships between external or internal nutrient inputs and phytoplankton dynamics (Burger et al., 2008; Cui et al., 2016; Li et al., 2015); (3) the interactions between phytoplankton and macrophytes (Asaeda et al., 2001).

2.4.2. Nutrients

Within the bibliographic corpus, numerous references, precisely 117 references (17%), 46 references (11%) and 74 references (17%), are marked respectively with the keywords “phosphorus”, “nitrogen” and “nutrient” (see Appendix A). These references do not necessarily focus on the modelling of nutrients only. Phosphorus is the most studied nutrient as it is generally considered as the main limiting nutrient of phytoplankton growth in most lakes (e.g. Schindler, 2006; Sondergaard and Jeppesen, 2007).

As for phytoplankton, some models – mostly the empirical and static ones – only represent the total phosphorus (Dillon and Rigler, 1974b, 1974a; Nürnberg and LaZerte, 2004; Seo and Canale, 1996) and/or the total nitrogen concentrations (Brown et al., 2000; Ji et al., 2014; Milstead et al., 2013; Reckhow, 1993).

However, to describe correctly the nutrient cycle and its dynamics, the different nutrient forms are often distinguished. The phosphorus is generally divided into two groups: particulate and dissolved phosphorus (Lung et al., 1976). Other models make the distinction between organic and inorganic nutrients (Deus et al., 2013). Among the dissolved inorganic nitrogen pool, nitrate and nitrite are often separated from the ammonium (Lindim et al., 2015; Wu et al., 2017), the nitrification and denitrification processes being considered as essential for the

ecosystem dynamics. In complex models such as CAEDYM (Hipsey et al., 2011), in addition to the forms previously mentioned (particulate/dissolved, organic/inorganic, nitrate/nitrite/ammonium), the organic compartments can also be divided into labile and refractory forms.

Finally the carbon, nitrogen and phosphorus contents of biological organisms such as zooplankton, phytoplankton, bacteria or macrophytes can be described through the use of either constant or variable stoichiometric ratios (see CAEDYM model (Hipsey et al., 2011)). Fernandez et al. (1997) introduced as model variables the soluble reactive, the soluble non-reactive and the particulate phosphorus cell quotas in phytoplankton, which are defined as phosphorus amount per biomass unit (Droop, 1968). The phosphorus content in shoots, secondary shoots and roots of macrophytes can also be included (Asaeda et al., 2000).

In order to simulate accurately the nutrient concentration dynamics in lakes, interactions between nutrients and other components of the ecosystem are often represented (Asaeda et al., 2001). Nutrient outputs through evaporation, denitrification and rivers or ground outflows can be included, as it is the case of nutrient external inputs coming from the watershed, the atmospheric deposition, the rainfall, and the ground. Some papers deal specifically with nutrients external loadings that are computed from watershed models such as SPARROW (Benoy et al., 2016; Milstead et al., 2013; Robertson and Saad, 2011), from specific models such as PCLoad (van Puijenbroek et al., 2004) or from satellite images (Politi and Prairie, 2018). In Liu (2013), an empirical model is introduced to estimate the nutrient release from industrial manufacturing, livestock breeding, crop agriculture, household consumption and atmospheric deposition. Nutrient internal loading is increasingly considered in the models (Burger et al., 2008; Li et al., 2015) as its impact on the lake nutrient concentrations and the phytoplankton growth limitation is now recognized (Wu et al., 2017). To simulate the internal cycling it can be necessary to take into account some bio-physical processes such as nutrient upwelling fluxes (Hamblin et al., 2003), sediment resuspension (Chung et al., 2009) and nutrient release from sediments (Riverson et al., 2013).

2.4.3. Sediment

About 10% of the references (46 references out of 438) have “sediment” as keyword. Sediment is an important pool of nutrients that play a key role in the nutrient cycles. Most of the models that specifically focus on sediment are 0D models, namely box-models (Chapra and Canale, 1991) or 1D vertical models (Chung et al., 2009; Gudimov et al., 2016). The main processes considered in these models are: (1) sediment diagenesis which refers to the set of biogeochemical processes within the sediment (Gudimov et al., 2016; Paraska et al., 2014); (2) sediment resuspension (Chung et al., 2009); (3) and nutrient and/or oxygen exchanges between the sediment and the water column (Smits and van der Molen, 1993; Snodgrass, 1987; Walker and Snodgrass, 1986).

2.4.4. Oxygen

The word “oxygen” appears in 46 of the 438 selected references, which represents 10% of the bibliographic corpus. Most of oxygen models are mechanistic (Antonopoulos and Gianniou, 2003; Bell et al., 2006; Bonnet and Poulin, 2004; Chapra and Canale, 1991), but some empirical models have also been developed (Chen and Liu, 2014; Elshaarawi, 1984; Rankovic et al., 2010). Oxygen dynamics is generally modelled by including one variable, the oxygen concentration, and several related processes. Depending on the other variables of the model, reaeration, aerobic respiration of living organisms, photosynthesis of plants, oxidation of the organic matter and denitrification can be included (Stansbury et al., 2008; Xu and Xu, 2016). Sometimes, sediment oxygen demand (SOD) is also represented (Antonopoulos and Gianniou, 2003; Deus et al., 2013; Terry et al., 2017), to account for the quantity of oxygen uptake by sediment when it is not explicitly

represented. In general, oxygen models are coupled with sediment models (Gudimov et al., 2016; Moore et al., 1996).

2.4.5. Cyanobacteria

The keyword “cyanobacteria” has been found in 35 references of the bibliographic corpus, which corresponds to 8% of the selected references.

According to many authors (e.g. Carey et al., 2012; Gkelis et al., 2014; Newcombe et al., 2012; O’Neil et al., 2012), eutrophication and climate change promote algal blooms and more specifically cyanobacterial blooms. Since the 1990s, cyanobacteria have been the subject of modelling works related to eutrophication (Easthope and Howard, 1999; Patterson et al., 1994), but the number of articles devoted to this subject has particularly increased since the mid-2000s. On the 5th of July 2018, the databases available on the Web of Science that we queried with the search equation “TITLE=((lake model*) AND (cyanobacter* OR bloom*))” gave a list of 71 references, more than 85% of which were written after 2005. The models of cyanobacteria range from simple regression models (Onderka, 2007) to 3D coupled hydrodynamic-ecological models (Carraro et al., 2012). Models that are dedicated to the prediction can be mechanistic but are mainly empirical (Carvalho et al., 2011; Cha et al., 2014) and increasingly based on “data-driven” approaches (Obenour et al., 2014; Zhang et al., 2015).

Cyanobacteria, which are prokaryotic phytoplankton, can be represented either with the same variable as phytoplankton (Shan et al., 2014) - in that case it is assumed to be dominant throughout the year - or as a sub-group of phytoplankton. In CAEDYM model (Hipsey et al., 2011) for example, phytoplankton can be decomposed into five groups: dinoflagellates, cyanobacteria, chlorophytes, cryptophytes and diatoms. Cyanobacteria can also appear under the name of “blue-green algae” as a sub-group of phytoplankton (e.g. Harada et al., 2013). Some specific processes of cyanobacteria are sometimes represented, as for example its flotation capacity in the water column (Aparicio Medrano et al., 2013; Walsby, 2005).

2.5. Model selection

The previous paragraphs give an overview of the different types of models that are used for the modelling of lake eutrophication. We can then wonder how to choose among these different types of models. Answering to this question is not simple, but general trends can nevertheless help our choice. The selection of the model type and structure will depend on the available knowledge and data, and on the modelling objective. With little knowledge about the ecosystem, only empirical models can be considered. Regression models can be obtained from few data and are useful to estimate mean annual values. On the other hand, data-driven models based on machine learning techniques require a large amount of data and manage to make short-term prediction. On the opposite, process-based models will be considered only if sufficient knowledge about the processes of the ecosystem is available. Data are nevertheless also required for such models, especially for the calibration of the model parameters. However, the results of process-based models can also be used for qualitative studies. In that case, the model outputs are validated by confrontation with the already acquired knowledge. Finally, when both knowledge and data are available, we can consider mixed approaches. For example, we can use a Kalman filter technique that requires data to adjust the parameters of a process-based model. Concerning the structure of the model, the variables to be represented are the variables of interest for the study, namely the variables that we want to simulate and the variables on which they depend. In the same way, we will represent the processes of interest and the ones that we assume to have an impact on the system we intend to represent. The time-scale of the targeted simulations will also determine the processes to be included. For example, it may be useless to take into account daily variations of some processes if we are interested on the annual variations of the ecosystem. Finally, depending on the level

of ecological description (individuals, species, populations, etc.), different types of models can be considered: individual based-models, population equations, meta-ecosystems.

3. Main results obtained with process-based models

In the sequel, we only review the results obtained with process-based models because this type of models is required when models are to be used in prospective scenarios. Indeed, for assessing ecosystem evolution, at long or mid-term, in response to local and global changes (e.g. climate change, urbanization, ...) or restoration actions, it is mandatory in our opinion that the main processes involved in the ecosystem functioning are taken into account.

Many eutrophication models of lake ecosystems have been applied to study sites for which monitoring data are available. Model description, including represented processes and equations, as well as calibration and validation results are presented in many articles (e.g. Bruce et al., 2006; Elliott and Thackeray, 2004; Elliott et al., 2007; Hamilton and Schladow, 1997; Leon et al., 2011; Lewis et al., 2002; Los and Brinkman, 1988; Reynolds et al., 2001a, 2001b; Riley and Stefan, 1988; Rukhovets et al., 2003). These models are mainly applied to simulate phytoplankton biomass, nutrients, oxygen, and in some cases cyanobacteria. The results of these models are given in the sequel.

3.1. Phytoplankton dynamics

Aimed at better understanding phytoplankton dynamics, process-based models are run at seasonal to multiannual time scales. The main issues addressed are as follows: biomass of the main phytoplankton groups and/or of total phytoplankton, total chlorophyll concentration, values at different depths or mean values in the epilimnion, phenology of phytoplankton blooms (biomass peak dates, duration of threshold overpass), etc.

Phytoplankton data are generally biovolumes of species identified by microscopy. Because of the long time necessary to obtain this type of data, the measurements are frequently performed in mean samples, for example collected in the euphotic layer or at a specific depth (Bruce et al., 2006; Elliott et al., 2007). Chlorophyll is frequently considered as a proxy of phytoplankton biomass. For example, the results of multiannual simulations over 11 years in Lake Erken (Sweden) are expressed as monthly mean total chlorophyll in the surface layer (0–10 m) (Elliott et al., 2007).

In large lakes, 3D modelling can be required. Hillmer et al. (2008) compare the results of 1D vertical (DYRESM-CAEDYM) and 3D (ELCOM-CAEDYM) models on the same study site, Lake Kinneret. Taking into account the horizontal heterogeneity of the lake makes it possible to obtain better results. In Lake Erie (Leon et al., 2011) mesoscale physical processes such as upwelling and general circulation in the lake have been modelled with the 3D ELCOM model. The spatio-temporal evolution of the variables is well simulated even if the authors underline the difficulty of comparing the simulation results of the phytoplankton succession with the measurements because of the necessary aggregation of the species in the model.

Concentrations of chlorophyll or carbon are derived from field measurements of biovolumes, by using conversion factors, which vary widely between authors. The quality of the phytoplankton biomass results, when evaluated in relation to the total chlorophyll concentration, is generally considered satisfactory. To judge the acceptability of the results, one criterion frequently used is that the model results remain within a range of two standard deviations from the mean of the measured values (Elliott et al., 2007).

Functional traits have been introduced in the definition of phytoplankton groups in order to better model the functional characteristics of an ecosystem and its responses to changes in nutrient inputs (Mieleitner and Reichert, 2008). This should also make the model more generic and allow better portability to other study sites.

Nevertheless the predictive capacity of these models remains modest. The ability of 124 models to replicate the dynamics of functional phytoplankton groups has been studied recently (Shimoda and Arhonditsis, 2016). The authors note a very large variability in the characterization of the functional phytoplankton groups as well as in the mathematical formulations that describe the main physiological processes of these groups (growth, nutrient absorption kinetics, mobility, etc.).

3.2. Cyanobacteria dynamics

Cyanobacteria strongly impair lake ecological functioning. Moreover they cause significant public health problems. Modelling their dynamics and the processes that control them are therefore the subject of many studies (Belov and Giles, 1997; Carraro et al., 2012; Elliott, 2012; Guven and Howard, 2006; Hense and Beckmann, 2006). According to many authors (e.g. Carey et al., 2012; Gkelis and Zaoutsos, 2014; Newcombe, 2012; O'Neil et al., 2012; Paerl and Huisman, 2008; Paerl and Paul, 2012), the ongoing climate change is likely to result in an increase in global cyanobacterial biomass as well as in occurrences of blooms.

Guven and Howard (2006) provide a review and critical analysis of 12 main models of cyanobacteria development in lake ecosystems. Two modelling approaches are discussed: deterministic models and neural network models. These models generally focus on describing either the biological processes involved in the growth of biomass or the processes involved in the motion of cells. Few people combine all the aspects that affect the dynamics of cyanobacteria.

Migration in the water column is a characteristic process of cyanobacteria: the rate of settling or flotation in the water column varies according to their density, which itself varies according to the amount of carbohydrates and volume of vacuoles in the cells. This is a very complex, non-linear process, with many feedbacks. It involves the intensity of photosynthesis, which is itself a function of the intensity of light in the water column, and therefore of the location of cyanobacteria in the water column. In addition, the different species of cyanobacteria form colonies whose morphometric characteristics affect the mobility. The models depict the migration process with different levels of complexity.

In Kromkamp and Walsby (1990), the density change depends on two simultaneous processes: an increase controlled by the light intensity received by the cells and a decrease as a function of time. The parameter values of the equations were obtained from experimental data of density change of a cyanobacterium species (*Planktothrix aghardii*) as a function of time and light intensity. The results show that the size of the colonies influences the migration rate but not the depth reached in the water column. The biomass vertical location fluctuates according to the rise of the floating colonies and the settling of others towards the bottom. Phosphorus deficient cells migrate to greater depths than light-limited cells.

Howard et al. (1996) propose a cyanobacterial growth and transport model that accounts for, on the one hand, the photosynthesis production, the cell density variation and the vertical migration of cells and on the other hand, the turbulent mixing in the water column that also affects cyanobacteria motion.

Belov and Giles (1997) present a dynamic model of cyanobacteria motion based on the properties of regulation of cell buoyancy under simplified conditions: an isothermal water column where nutrients are not limiting factors. The main factor controlling cell mobility is the nycthemeral cycle of light. The article focuses on analysing under these conditions the mathematical behaviour of the equations involved in the model.

One of the specificities of cyanobacteria is the ability of certain species, the diazotrophic species, to fix atmospheric nitrogen. Accounting for this process allows the models to better represent the control of the succession of species by the available nutrients. Hense and Beckmann (2010) propose several versions of a model of the life cycle

of diazotrophic cyanobacteria, considering the active phase of nitrogen fixation and the vegetative phase of cells. The ecological characteristics, life cycle of cyanobacteria and interactions with hydrodynamics are particularly complex (Fig. 2). The simplified approach satisfactorily describes the dynamics of cyanobacteria, in particular the time patterns of blooms and the intensity of nitrogen fixation. The proposed set of equations can be inserted into different types of lake models of cyanobacterial dynamics.

In Lake Pusiano, Carraro et al. (2012) validated the 3D model ELCOM coupled to the CAEDYM biological model with high frequency measurements to identify the factors, including hydrodynamic factors, which drive the spatial distribution of the cyanobacterium *P. rubescens*.

Regarding the impact of climate change on cyanobacteria, Elliott (2012) reviewed different predictive models. Most of the analysed results show an increase in the relative biomass of cyanobacteria due to an increase in water temperature, an increase in residence time and an increase in nutrient loading from the watershed. The main effect of climate change is to alter the phenology of cyanobacterial blooms and the abundance of their biomass. The lake food web is also changing due to the low nutritional value of cyanobacteria for zooplankton.

3.3. Integration of models in early warning system

For management applications, models are often integrated into warning systems to predict short-term phytoplankton blooms, particularly to improve operational control of cyanobacterial blooms (Shimoda and Arhonditsis, 2016). Most articles describe the models used and the architecture of the system. But few *a posteriori* comparisons of the forecasts with measurements made afterwards, are performed.

In order to predict algal blooms in Lake Taihu, the EcoTaihu model has been integrated into a Windows software platform (Zhang et al., 2013). The results of the simulations generally show a good agreement with the measurements. But the authors also point out that no model is able to integrate all ecological processes. The forecast discrepancies are not only due to the model but also to data uncertainties and because modelling results and field measurements are not directly comparable.

3.4. Ecosystem response to local management strategies

Eutrophication models can be used to study prospective scenarios and compare the impact of local management alternatives. Several management scenarios of Los Molinos reservoir (Argentina) were tested with a model describing the dynamics of nutrients and phytoplankton (Rodriguez Reartes et al., 2016). After calibration and validation of the model, scenario simulation results highlighted the impact on water quality of livestock husbandry practices and of insufficient wastewater treatment, especially septic tanks. According to the model simulations, the combination of wastewater treatment in the reservoir direct watershed and measures to reduce nutrient loading (N and

P) from livestock would be the most beneficial to preserve the quality of the lake.

The effects of different actions to reduce eutrophication of a lake in Sweden (reduction of nutrient inputs, biomanipulation, herbicide application) were analysed with a vertical 1D biogeochemical model (Pers, 2005). According to the simulation results, the best effects are obtained with a nutrient reduction and biomanipulation of the fish species.

The comparison of different prospective scenarios should include a reference scenario. This is not the case in most of the performed modelling studies. This is due to the lack of sufficiently long-term historical data sets. Moreover, it is particularly complex to achieve a reliable assessment of the environmental conditions prior to the onset of eutrophication. For total phosphorus, reference values of the watershed loading can be estimated by different approaches (export coefficients, morpho-edaphic indices, paleolimnological estimates). But the results of these different methods have rarely been compared. A study performed on 35 sub-alpine lakes in northern Italy (Salerno et al., 2014) highlighted the need of deterministic watershed models to estimate the total reference phosphorus inputs.

An expected outcome of the prospective simulations regards the level of nutrient loading by the watershed that must not be overpassed to avoid eutrophication of a lake. But even when the targets to be achieved are derived from modelling results, the authors remind that these values must be considered with caution as the models are not able to anticipate accurately the changes in the trophic web that would occur in response to nutrient reduction (e.g. Trolle et al., 2008).

Modelling studies mainly focus on the advantages of the modelling approach developed and its transferability to other systems. The model is generally implemented on a particular study site for which a sufficient data set exists. Despite the transferability of process-based models, they must be implemented in a configuration adapted to the characteristics of each lake in order to estimate the required threshold of nutrient loading (Trolle et al., 2008). Moreover, due to the complexity of the ecological functioning of lake ecosystems, many processes are not taken into account or are very simplified in the models (role of sediment, change of phytoplankton assemblages, mobility of certain species, etc.). When recommendations are made, the authors are very cautious and they immediately nuanced the recommendations. Thus, the total phosphorus loading which would allow Lake Ravn (Denmark) to achieve the objectives of good ecological status required by the European Framework Directive on Water, was estimated thanks to a vertical 1D model (Trolle et al., 2008). The authors recommend a reduction of at least 50% of the total phosphorus inputs by the watershed. In parallel, they raise awareness on the possible cascade effects within the food web, not simulated by the model, and which could lead to an unpredictable evolution of the ecosystem.

3.5. Ecosystem response to global changes

A common application of models is the study of expected effect of global changes, especially climate change. Climate change will impact precipitation patterns, wind speeds, solar radiation, and air temperature (e.g. Arnell and Gosling, 2013; Beniston et al., 2007; European Environment Agency, 2012). Most models simulate the effect of climate change on different aspects of lake functioning related to eutrophication: mainly oxygen concentrations (Fang and Stefan, 1997, 2009), phytoplankton growth (Hassan et al., 1998) and the dominance of cyanobacteria (e.g. Elliott, 2012). The consideration of climate change is mainly based on two approaches: (1) the use of outputs from regional climate models treated by downscaling techniques to obtain meteorological forcing at the studied lake level; or (2) a meteorological forcing sensitivity analysis where actual measured meteorological data are modified by a range of factors.

Very often the analysis of the influence of climate change, in particular of global warming, focuses on cyanobacteria. Global warming is supposed to have a positive effect on the increase of cyanobacteria

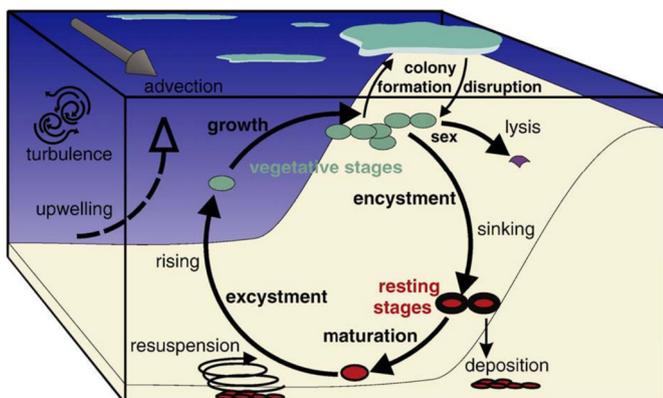


Fig. 2. General sketch of main steps of cyanobacteria life cycle (Hense, 2010).

biomass (e.g. Carey et al., 2012; Newcombe, 2012; Paerl and Paul, 2012; Posch et al., 2012; Wagner and Adrian, 2009). Nevertheless, very few reliable predictive simulations of the dominance of cyanobacteria have still been performed (Elliott, 2012).

In Lake Windermere (Great Britain), the effect of an increase in water temperature and phosphorus loading on phytoplankton has been studied with the PROTECH model (Elliott, 2011). The results show an earlier spring peak of diatoms (2–3 days/°C). The biomass of diatoms, which is controlled mainly by light is little changed. On the other hand, the biomass of cyanobacteria increases with the increase of the two factors studied. These two factors act in synergy, the predominant influence being due to phosphorus inputs. The dominance of cyanobacteria is enhanced in late summer. Temperature impacts mainly succession and seasonal phytoplankton community whereas nutrient inputs affect the amount of produced biomass.

Howard and Easthope (2002) used the predictions of the HADCM2 climate model over a period of 90 years, until the end of the 21st century, to simulate the evolution of the growth of the cyanobacterium *Microcystis* in Farmoor Lake (Great Britain). The main meteorological variables used are the monthly averages of wind speed, cloud cover and solar radiation. The results do not show an overall increase in the annual biomass of cyanobacteria. On the other hand, the growth period of cyanobacteria would be longer with higher biomass than currently in spring (May) and autumn (September). These results only quantify the direct effect of climate change because the long-term change in rainfall on loading from the watershed is not taken into account.

The effect of global warming predicted until the end of the 21st century has been studied in three lakes in New Zealand (Trolle et al., 2011b). A regional climate model based on the IPCC A2 scenario predicts an average annual increase in air temperature of about 2.5 °C in the 2100s in the studied lake region. The future climate conditions are described in a very simplified way; only the change of air temperature is taken into account. The average annual increase in air temperature forecast for the year 2100 has been added to the average daily temperatures over the period 2002–2007. The morphometric and trophic characteristics of the three modelled lakes are different. The first is quite deep (33.5 m) and oligo-mesotrophic, the second shallow (13.5 m) and eutrophic and the third very shallow (2.5 m) and very eutrophic. Cyanobacteria are present only in the second lake. Modelling results show an increase in phytoplankton biomass in summer and an increase in the dominance of cyanobacteria in the second lake. The average annual biomass increases in the oligo-mesotrophic and eutrophic lakes but decreases in the highly eutrophic lake. The phytoplankton biomass decreases in winter and spring, especially diatoms.

A recent analysis of ten modelling studies (Elliott, 2012) on the impact of climate change on cyanobacteria has shown an increase in the relative abundance of cyanobacteria with an increase in water temperature, an increase in the residence time of the water and an increase in nutrient loading by the catchment.

The direct effects of climate change mainly relate to phenology of phytoplankton dynamics but little to the annual amount of total biomass. These changes in phytoplankton succession may result in nitrogen limitation in some lakes, and thus favour the dominance of nitrogen-fixing cyanobacteria. In addition, warmer water in spring can increase nutrient uptake by the phytoplankton community, which in some lakes causes nitrogen limitation later in the year, potentially favourable for some nitrogen-fixing cyanobacteria. The increase in the relative abundance of cyanobacteria may also impact the higher levels of the ecosystem food web due to the low grazing of cyanobacteria by zooplankton.

3.6. Coupled models of lake and watershed

Coupling watershed modelling and lake response modelling is a key issue for an efficient use of models in eutrophication control. But to our knowledge, few research results are still available.

Most often, the coupling between watershed model and lake model is not effective. A hydrological model of Lake Cayuga watershed (USA) has provided estimates of nutrient loading by lake tributaries (Haith et al., 2012). But this watershed model is not coupled with a model of the lake itself. This is also the case for Lake Gucheng watershed in China (Huang et al., 2009) or for Lake Tahoe watershed (USA) (Riverson et al., 2013).

Since the 2000s, integrated modelling of the watershed and the lake has been undertaken. Lake watershed modelling is conducted with the objective of providing the lake model with input data to then simulate the lake response to watershed loadings. But the limits of these coupled models come from the cumulative uncertainties of the hydrological model and the lake model. If the inflows are fairly well simulated, the main uncertainties are due to errors in computing nutrient concentrations in the lake tributaries (Liu et al., 2006; Silva et al., 2016; van Puijenbroek et al., 2004).

Carraro et al. (2012) propose for Lake Pusiano (Northern Italy) a coupled model of loading by the watershed (SWAT model) and a deterministic model of the lake response (DYRESM-CAEDYM model). The results obtained for different scenarios are discussed and compared, but no quantified recommendation for a percentage of reduction in loadings or concentrations to be achieved is given.

Very few studies have focused on coupling climate, watershed and lake models. To study phytoplankton biomass in a large shallow lake, Lake Malaren (Sweden), a regional climate model, a hydrological model, and a lake model were used in sequence (Markensten et al., 2010). In this lake, warming increases the duration of phytoplankton production, slightly increases total biomass, and modifies the phytoplankton composition to the advantage of nitrogen-fixing cyanobacteria. According to the authors, the change in the hydrological regime and therefore the nutrient loading to the lake drives the dominance of cyanobacteria.

The aquatic continuum, from headwaters to the ocean, is at the heart of current research on biogeochemical processes in inland waters. This is reflected in the topic of the special issue of Limnology and Oceanography, a reference journal in the field, entitled “Headwaters to oceans: ecological and biogeochemical contrasts across the aquatic continuum” (Xenopoulos et al., 2017). In this area, progress on knowledge integration is rapid and modelling of the continuum, still in its infancy, should make significant progress in the coming years.

4. Discussion and perspectives

The development of lake eutrophication models is still a growing field in limnology. However several authors complain that the performances of the biological models remain relatively low (Mooij et al., 2010; Shimoda and Arhonditsis, 2016). According to Trolle et al. (2011a), the problem is not the “lack of knowledge about ecosystem functioning, but rather the limited extent of open communication, inadequate collaboration and lack of suitable structure to support the aquatic scientific modelling community”. In their paper, these authors argue for the adoption of good practices for developing, using and sharing models effectively and correctly, which should help improving the models. Mooij et al. (2010) identified two challenges for making further progress in lake ecosystem modelling: to avoid developing more models largely following the concept of others (‘reinventing the wheel’) and to avoid focusing on only one type of model, while ignoring new and diverse approaches that have become available (‘having tunnel vision’) (Mooij et al., 2010). This suggests to merge different modelling approaches, such as 1D hydrodynamic-ecological model and super individual-based model (Makler-Pick et al., 2011), or machine learning models and physical dynamical models (Crisci et al., 2017).

To improve the models, the complexity of the predictive ecosystem models should also be increased, because “there is a lot of knowledge that we are not using” (Hellweger, 2017). The most striking example is the almost systematic use of the Monod function for representing

the growth of a phytoplankton population whereas the use of internal (vs. external) nutrient quota (Droop, 1968) could be represented (Hellweger, 2017). Another example is the use of Michaelis-Menten kinetics for nutrient uptake by phytoplankton, which does not enable to represent the variable stoichiometry of biomass and of nutrient uptake (Flynn, 2010, 2005; Smith et al., 2014) whereas size- and trait-based kinetics give promising results (Fiksen et al., 2013; Smith et al., 2014). In the same way, the process of mineralization of the organic matter by bacteria, which has been proved to be important for the cyanobacteria dynamics, is often represented as a simple chemical reaction with a rate either constant or dependent on the bacteria concentration at best (Y. Li et al., 2014). Xu et al. (2015a, 2015b) also claim that the use of more advanced statistical methods, such as quantile regression, can improve the models of lake eutrophication.

Even if the relationship between complexity and uncertainty of models is not so clear (Håkanson, 1995; Hellweger, 2017; Jørgensen, 1990), it is obvious that the outcomes of simulated scenarios are limited by great uncertainty (Arhonditsis and Brett, 2004). Some authors have attempted to quantify model errors due to uncertainty (Bennett et al., 2013; Hongping and Yong, 2003; Reckhow, 1994; Scavia et al., 1981; Snodgrass, 1985; Stow et al., 1997; Van Straten and Keesman, 1991), but few models include thorough uncertainty analyses (Hongping and Yong, 2003).

This uncertainty partly comes from the large set of parameters (sometimes more than 100) to be calibrated. To quantify the effect of parameter uncertainties on the model outputs, sensitivity analysis can be conducted (Arhonditsis et al., 2007; Brett et al., 2016; Janse et al., 2010; Yi et al., 2016). However, as for general uncertainty analysis, sensitivity analysis is not always performed. Two articles (Arhonditsis and Brett, 2004; Shimoda and Arhonditsis, 2016) have investigated whether the conventional methodological procedures for sensitivity analysis, calibration and validation, are reported in the papers or not. They show that only half of the papers present sensitivity analysis results and that “manual” or “trial and error” calibration is the most applied calibration procedure. Very few papers use automatic calibration procedures that are either based on optimization or on Monte Carlo and Bayesian inference. Moreover these papers only deal with 0D or 1D models.

Another part of output uncertainty comes from the model structure itself. To reduce it, several “ensemble approaches” have been proposed, similar to those used for weather forecasts. In (Gal et al., 2014; Nielsen et al., 2014) an ensemble of model runs obtained with several “equivalent” set of parameters are used to improve the model predictive power. In (Trolle et al., 2014), the same scenario is simulated using an ensemble of models. Bayesian model averaging (BMA) can also be used to improve the predictive performance of the models (Hamilton et al., 2009).

Another effective way is to conduct cross-comparisons of similar models on the same study sites. This type of comparative studies has been performed recently for 1D models (Bruce et al., 2018; Perroud et al., 2009; Stepanenko et al., 2012, 2010). To our knowledge very few attempts have been made for hydrodynamic-ecological models (Trolle et al., 2014) and none for 3D models.

Nevertheless, to perform such studies, portability of the model software is required. This type of concern is just starting to be addressed by the modeller community. A Fortran-based Framework for Aquatic Biogeochemical Models (FABM - Bruggeman and Bolding, 2014; Trolle et al., 2011a, 2011b) enables to easily couple hydrodynamic models with ecological models, whereas the project “Framework for Interoperable Freshwater Models” (FIFM) has investigated flexible computer-based frameworks for integrating freshwater models (Elliott et al., 2014). The Database Approach To Modelling (DATM - Mooij et al., 2014) enables to automatically implement the same model under different frameworks. In order to facilitate the comparison of models or the application of one model on several lakes, it is also necessary to share the codes and the data sets (Mooij et al., 2010). Just as importantly, the data sets must be of good quality and enriched with meta-information (such as the type of sensor used and their accuracy). This is mandatory for the

good interpretation and use of the data (Mooij et al., 2010). The use of high-frequency sensors (Brentrup et al., 2016; Carraro et al., 2012; Soullignac et al., 2017), as well as satellite images (Curtarelli et al., 2015; Dash et al., 2011; Tyler et al., 2006; Yacobi, 2006), will also enrich significantly the data sets. Using such enriched and good-quality data sets can improve the model performances. Indeed, the more data we use for calibration, comparison with model outputs or to feed machine learning models, the greater the accuracy of the model will be.

5. Conclusion

Early lake eutrophication models in the 1970s were empirical models linking in-lake phosphorus and chlorophyll concentrations, as well as models of watershed nutrient loading and in-lake chlorophyll concentration. These models, very easy to implement, were useful for providing targets of nutrient and chlorophyll concentrations, required for reducing or controlling lake eutrophication. Dynamic deterministic models have been then developed, whose characteristics are very diverse as regards the spatial dimension (well-mixed system, 1D vertical to 3D models), the sediment exchange with the water column, the complexity of ecological functioning and the hydrodynamics. Most of these models represent the pelagic zone of the lake. The most represented state variables include phytoplankton, considered as a single group or divided into main groups, nutrients (phosphorus and nitrogen) and oxygen. Among the phytoplankton groups, cyanobacteria have been increasingly represented since the mid-2000s. The dynamics of macrophytes and their possible competition with phytoplankton are accounted for in some rather recent models. One notable development over the past decade has been the modelling of phytoplankton dynamics based on the functional traits of dominant species. The objectives of the modelling studies are frequently related to the assessment of the expected mid-and long-term evolution of lake eutrophication under the influence of global changes (nutrients, urbanization, climate...). Among these changes, the effects of global warming are the most frequently addressed. At these time scales, a main barrier that models have to face, regards the evolution of the phytoplankton succession and its cascading effects on lake ecological functioning. Recent evolutions show a strong coupling between modelling and acquisition of new types of experimental data (remote sensing, high frequency field sensors, biology molecular data...). A strong trend seen in papers published in the last decade is the increasing number of application of 3D models coupled with satellite images of phytoplankton biomass spatial distribution.

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Appendix A

In this appendix, we first give some details about the method applied for obtaining the bibliographic corpus considered in this review. We then present some simple statistics about: (1) the number of publications and citations; (2) the general categories, research areas and journal titles; (3) the keywords of the references included in the bibliographic corpus.

A.1. Selection of the bibliographic corpus

The present review was performed, using the bibliographic search tool proposed by Web of Science. The first database search of February 2017 (Crave et al., 2017) was updated on 1st June 2018 with the following search equation:

TITLE=((eutrophic* OR oxygen* OR hypox* OR anox* OR phytoplankton* OR “harmful alga”* OR nutrient* OR cyanobact* OR proliferat*) AND (model* OR numerical* OR simulat*) AND (lake* OR reservoir*))

All citation databases were consulted for all available years (from 1956 to 2018). Among the references obtained, we kept only the journal articles written in English. This query provided us with a list of 487 references from which we removed 49 references that were not relevant. We finally get a bibliographic corpus of 438 references among which 431 references are indexed in the Web of Science core collection, 62 in the MEDLINE database, 1 in the KCI Korean Journal Database and 1 in the Scientific Electronic Library Online (SCIELO) database. Each reference may be indexed in several databases.

A.2. Number of publications and citations

The first referenced paper (Droop, 1968) was published in 1968. Since then, the number of publications per year has obviously increased (Fig. 3), following the global tendency observed for the total number of scientific publications. In average, 8.6 articles were published per year, and each article was cited 17 times. The total number of citations is 7447, which corresponds, since 1968, to a mean value of 146 citations per year.

A.3. General categories, research areas and journal titles

The repartition of the references is given in terms of general categories, research areas and journal titles (Table 2). We note that most of the references of the bibliographic corpus come from the “science technology” and “life sciences biomedicine” categories. This shows that the studies are motivated both by academic objectives to improve knowledge and by more applied objectives to develop management strategies (see Section 2.2). One third of the references (respectively one quarter) also belongs to the category of “physical sciences” (respectively “technologies”), knowing that one reference may belong to several categories.

The repartition according to the research areas shows that lake eutrophication modelling is a multi-disciplinary field of research. Most of the references (two thirds) are in the field of “environmental sciences and ecology”, but the research areas of “marine and freshwater biology”, “water resources” and “engineering” also contain a significant number of references (from 20 to 30%). Note that some publications in “mathematics” and “computer science” are also included in the bibliographic corpus, which is not surprising as we focus on modelling studies.

The journal in which most papers (16%) have been published is “Ecological modelling”, perhaps because it is one of the few journals in environmental sciences that only focus on modelling. The scope of the other most represented journals cover the research area of water sciences in general, without restriction to modelling approaches.

Table 2

Repartition of the publications according to their general categories, their research areas and the journal title (provided by Web of Science). Only the research areas (respectively the journal titles) that represent more than 2% (respectively 1.5%) of the bibliographic corpus are listed.

	Records	% of 438
General categories		
Science technology	435	99.3
Life sciences biomedicine	363	82.9
Physical sciences	154	35.2
Technology	99	22.6
Social sciences	2	0.5
Research areas		
Environmental sciences and ecology	272	62.1
Marine and freshwater biology	141	32.2
Water resources	101	23.1
Engineering	86	19.6
Geology	30	6.8
Oceanography	22	5.0
Mathematics	10	2.3
Computer science	9	2.1
Journal titles		
Ecological Modelling	70	16.0
Hydrobiologia	25	5.7
Journal of Great Lakes Research	25	5.7
Water Research	18	4.1
Water Science and Technology	13	3.0
Limnology and Oceanography	12	2.7
Water Resources Research	11	2.5
Lake Reservoir Management	11	2.5
Ecological Engineering	8	1.8
Freshwater Biology	7	1.6
Science of the Total Environment	7	1.6

A.4. Keywords

An automatic search routine was implemented to sort the keywords according to the number of publications in which they appear. The routine does not search for an exact match but for an inclusion. For example a publication with “lake models” as keyword will be counted for the keywords “lake model”, “models”, “model” and “lake”. Only the keywords that appear in more than 20 publications of the bibliographic corpus have been considered. The obtained sorted list has then been divided in sub-groups as presented in Table 3. Not surprisingly the most common keywords are “lake”, “water” and “eutrophic”.

This classification of the keywords give an interesting overview of the research works presented in the analysed bibliographic corpus.

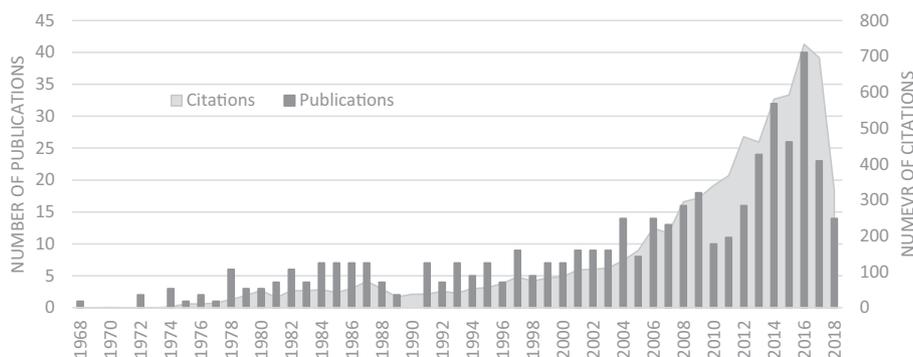


Fig. 3. Number of publications and citations per year, based on the ISI Web of Science citation report.

Table 3

Classification of keywords according to the number of publications in which they appear.

Study sites		Objectives		What is represented in the model		Study of the impact of ...	
226	Lake	54	Management	117	Phosphorus	33	Load
213	Water	49	Simulation	115	Phytoplankton	32	Environment
147	Eutrophic	31	Prediction	74	Nutrient	31	Climate
55	Reservoir	22	Restoration	56	Sediment	26	Temperature
46	River			46	Nitrogen	22	Light
39	Shallow	Methods		46	Oxygen	on ...	
27	Erie	229	Model	44	Chlorophyll	97	Water quality
25	Fresh water	21	Regression	35	Cyanobacteria	64	Dynamics
24	Bay	21	Sensitivity analysis	34	Iron	47	Ecosystem
21	Great lakes			27	Algae	37	Growth
				23	Zooplankton	29	Blooms

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