1 **Title**

2 Using 3D modeling and remote sensing capabilities for a better understanding of spatio-temporal
3 heterogeneities of phytoplankton abundance in large lakes

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Abstract

Lake biological parameters show important spatio-temporal heterogeneities. This is why explaining the spatial patchiness of phytoplankton abundance has been a recurrent ecological issue and is an essential prerequisite for objectively assessing, protecting and restoring freshwater ecosystems. The drivers of these heterogeneities can be identified by modeling their dynamics. This approach is useful for theoretical and applied limnology. In this study, a 3D hydrodynamic model of Lake Geneva (France/Switzerland) was created. It is based on the Delft3D suite software and includes the main tributary (Rhône River) and two-dimensional high-resolution meteorological forcing. It provides 3D maps of water temperature and current velocities with a 1 h time step on a 1 km horizontal grid size and with a vertical resolution of 1 m near the surface to 7 m at the bottom of the lake. The dynamics and the drivers of phytoplankton heterogeneities were assessed by combining the outputs of the model and chlorophyll-a concentration (Chl-a) data from MERIS satellite images between 2008 and 2012. Results highlight physical mechanisms responsible for the occurrence of seasonal hot-spots in phytoplankton abundance in the lake. At the beginning of spring, Chl-a heterogeneities are usually caused by an earlier onset of phytoplankton growth in the shallowest and more sheltered areas;

41 spatial differences in the timing of phytoplankton growth can be explained by spatial variability in
42 thermal stratification dynamics. In summer, transient and locally higher phytoplankton abundances
43 are observed in relation to the impact of basin-scale upwelling.

44 **Keywords**

45 3D modeling; remote sensing; chlorophyll-a; spatio-temporal heterogeneity; Lake Geneva; Delft3D

46 **Introduction**

47 In a world where lakes provide multiple services to society while facing strong anthropogenic
48 pressures, the protection and restoration of inland water bodies has become a critical political and
49 scientific issue. For example, the European Water Framework Directive obliges member countries to
50 take steps to reach a good ecological status for all their surface waters (European Commission, 2000).
51 To reach these challenging goals, the scientific and lake management communities aim to deepen the
52 understanding of lake ecological functioning, using ongoing lake monitoring efforts (Stewart et al.,
53 2016).

54 Phytoplankton, at the base of the food chain, controls to a fair extent the quality of the ecosystem
55 services and is widely used as an indicator of ecosystem health and sustainability (Xu et al., 2001).
56 However, evaluating the abundance and composition of this community in routinely obtained water
57 samples raises several issues regarding the representativeness of the collected lake samples since
58 phytoplankton is rarely homogeneously distributed over a water body (Pelechaty and Owsianny,
59 2003). This is all the more true in large and/or deep lakes (Leoni et al., 2014; Viljanen et al., 2009).

60 Understanding the mechanisms that drive plankton spatial distribution has been a recurring theme in
61 aquatic ecology and has been studied for several decades (Arhonditsis et al., 2004). Commonly,
62 phytoplankton spatial heterogeneities fall into two categories, vertical and horizontal distributions.
63 Phytoplankton can only develop in the upper part of the water column where solar energy is high
64 enough to support net photosynthesis (Reynolds, 1997), leading to the concepts of critical depth and
65 turbulence (Huisman et al., 1999). Still, important gradients across the euphotic zone in both the
66 abundance and composition of phytoplankton are frequently observed in deep lakes (Pomati et al.,
67 2011). The vertical distribution of chlorophyll-a concentration (Chl-a) in deep lakes is often
68 characterized by the presence of a deep Chl-a maximum which acts as a local hotspot of primary
69 production. The occurrence and the structure of a deep Chl-a maximum is only now beginning to be
70 properly understood (Leach et al., 2018). Heterogeneities along the horizontal axis – that have been
71 observed using traditional multi-site measurements and more recent techniques such as microwave
72 or optical remote sensing from space – remain equally difficult to explain because of the complexity of
73 the underpinning processes and mechanisms that are the basis of these heterogeneities (Moreno-
74 Ostos et al., 2007). Indeed, the distribution of phytoplankton is strongly affected by wind-driven
75 currents and also by spatial heterogeneity on environmental conditions (Cyr, 2017; Huang et al., 2014).

76 Despite the demonstration of lake patchiness in satellite observations, horizontal variability in lake
77 water parameters is often neglected. Samples used for lake monitoring and water quality assessment

are usually collected at a single station, often the deepest point of the lake, because this area is generally located in the center of the lake where anthropogenic impact and effect are limited. Nevertheless, the recent remote sensing capabilities can facilitate the description and to some extent, depending on the frequency of suitable images, the study of dynamics in lake heterogeneity (Bresciani et al., 2011; Gons et al., 2008; Kauer et al., 2015; Odermatt et al., 2012; Palmer et al., 2015). In large lakes, surface horizontal heterogeneities in Chl-a are a frequent phenomenon and also present structures that could change rapidly (Kiefer et al., 2015). Thus, the existence of such heterogeneities might raise several issues when studying the impact of local and global forcing on phytoplankton that requires a better understanding of the underlying mechanisms responsible for those heterogeneities (Chen et al., 2003). This is not just a matter of academic interest because the distribution of blooms of harmful cyanobacteria across lakes is of prime importance for risk assessment and management and affects the use of lakes for drinking water and recreation (Ibelings et al., 2003).

The physical properties of water govern its response to mechanical energy inputs, such as wind, river inflow and heat exchanges, resulting in vertical gradients of physical and chemical characteristics, such as temperature and nutrients, which are major factors controlling phytoplankton development. As such these physical processes may promote spatial heterogeneities in phytoplankton (Reynolds, 1997). Accordingly, we postulate here that a good understanding of physical dynamics is essential to explain the spatial heterogeneity observed in phytoplankton abundance. To test this, we applied a three-dimensional (3D) hydrodynamic model to Lake Geneva (France/Switzerland) and evaluated the ability of this hydrodynamic model to explain horizontal patchiness in phytoplankton abundance. For that purpose, we analyzed the vertical thermal structure predicted by the model at different stations in the lake when Chl-a presented strong surface heterogeneities. The role of hydrodynamic processes was expected to be strong enough that considering hydrodynamics alone would be sufficient to explain some of the phytoplankton heterogeneity patterns observed in Lake Geneva from 2008 to 2012. In other words, the purpose of this study is to show that by considering only hydrodynamics, we are able to explain and predict certain surface phytoplankton heterogeneities that are observed in lakes.

Materials and methods

Study site

Lake Geneva is a large and deep peri-alpine lake located in the western part of the Alps, on the border between France and Switzerland (Fig. 1 and Table 1). According to the international commission for the protection of Lake Geneva (CIPEL), it is thermally stratified during much of the year, never freezes over and does not undergo complete mixing every year. Its main tributary is the River Rhone which

with 184.3 m³/s, accounts for 85% of the total inflow (average from 1965 to 2015). The lake is monitored as part of a long-term in situ monitoring program by CIPEL for water quality (e.g. water temperature, Chl-a, transparency) and biological compartments, including the phytoplankton. This monitoring revealed important changes in phosphorus concentrations. In fact, Lake Geneva was eutrophic for several years in the 1960s and measures to reduce phosphorus in its watersheds were first implemented in the 1970s, leading to a decrease in phosphorus concentrations starting in the early 1980s. Nowadays, Lake Geneva is mesotrophic (Jacquet et al., 2014a).

Data

In this study, in situ vertical profiles of Chl-a and water temperature (WT), transparency and remote sensed surface Chl-a maps are used between 2008 and 2012. In situ Chl-a, WT and transparency are available from the CIPEL monitoring program. Sampling takes place at two stations, at the deepest point of the lake in the large basin (monitoring station SHL2: WGS84 6.58872° E, 46.45270° N; depth: 309 m) and in the small basin (monitoring station GE3: WGS84 6.21994° E, 46.29721° N; depth: 72 m) (Fig. 1). At SHL2, sampling is conducted twice a month, except in winter, when it is carried out only once a month. At GE3, sampling frequency is once a month throughout all the year. Samples for Chl-a measurements are collected at 10 depths: 0, 1, 2, 3.5, 5, 7.5, 10, 15, 20 and 30 m. Cells are collected on a Whatman GF/C filter (47 mm) and sonicated. The pigments are extracted with 90 % (v/v) acetone/water and the solution is filtered through a glass fiber filter GF/C (25 mm). Chl-a is measured by spectrophotometry (Strickland, 1968). WT is measured using multiparameter probes, SST-CTD009, SST-CTM214 and RBR-XRX-620. The transparency is measured as Secchi disk depth (SDD) which corresponds to the depth at which the light intensity in the water column is 15% of the intensity of the surface (Lemmin, 1995). Remotely sensed Chl-a is available from Kiefer et al. (2015). It was derived from satellite MERIS observations and the processing was done with the FUB WeW neural network algorithm (Schroeder et al., 2007). The algorithm gives a resolution of 260 × 290 m and can handle Chl-a concentrations between 0.05 and 50 µg/l. Data availability is summarized (Fig. 2).

Delft3D model

The open source Delft3D software used in this study has been widely applied for lakes of different sizes all around the world (Chanudet et al., 2012; Kacikoc and Beyhan, 2014; Li et al., 2015; McCombs et al., 2014; Soulignac et al., 2017; Wahl and Peeters, 2014). A previous modelling effort was performed on Lake Geneva by using Delft3D. It is presented in a series of three articles (Razmi et al., 2013, 2014 and 2017) (the references are given below). We chose the same surface heat flux module, the same bottom and surface roughness formula, the same meteorological inputs and the same Rhone River inputs. We

also simulated Lake Geneva entirely. But whereas Razmi and coauthors divided each year into four periods of three months, our objective was to run one-year simulations to cover the whole thermal stratification period. Also, they used a very fine grid (the lake surface was meshed using 45,000 grid cells) to study the small-scale hydrodynamics in the Vidy bay, a small part of the lake located in front of Lausanne, and they used a non-uniform vertical mesh (sigma-model). However, we wanted a model requiring less computational time, a regular resolution throughout the lake and a uniform vertical mesh to better describe the thermal stratification. For these reasons, we decided to create a new model of Lake Geneva. Delft3D has several modules (e. g.: hydrodynamics, water quality, etc.). In this study, only the hydrodynamic module Delft3D-FLOW was used. It solves the Navier-Stokes equations for an incompressible fluid, under the shallow water and the Boussinesq equations. The system of equations consists of the continuity equation,

$$\frac{\partial u}{\partial x} + \frac{\partial v}{\partial y} + \frac{\partial w}{\partial z} = 0,$$

the two horizontal equations of motion,

$$\frac{\partial u}{\partial t} + u \frac{\partial u}{\partial x} + v \frac{\partial u}{\partial y} + w \frac{\partial u}{\partial z} = -\frac{1}{\rho_0} \frac{\partial p}{\partial x} + \frac{\partial}{\partial x} \left(\nu_H \frac{\partial u}{\partial x} \right) + \frac{\partial}{\partial y} \left(\nu_H \frac{\partial u}{\partial y} \right) + \frac{\partial}{\partial z} \left(\nu_V \frac{\partial u}{\partial z} \right) + f v \text{ and}$$

$$\frac{\partial v}{\partial t} + u \frac{\partial v}{\partial x} + v \frac{\partial v}{\partial y} + w \frac{\partial v}{\partial z} = -\frac{1}{\rho_0} \frac{\partial p}{\partial y} + \frac{\partial}{\partial x} \left(\nu_H \frac{\partial v}{\partial x} \right) + \frac{\partial}{\partial y} \left(\nu_H \frac{\partial v}{\partial y} \right) + \frac{\partial}{\partial z} \left(\nu_V \frac{\partial v}{\partial z} \right) - f u,$$

the vertical equation of motion being reduced to the hydrostatic pressure equation, and the transport equation of heat,

$$\frac{\partial T}{\partial t} + u \frac{\partial T}{\partial x} + v \frac{\partial T}{\partial y} + w \frac{\partial T}{\partial z} = \frac{\partial}{\partial x} \left(D_H \frac{\partial T}{\partial x} \right) + \frac{\partial}{\partial y} \left(D_H \frac{\partial T}{\partial y} \right) + \frac{\partial}{\partial z} \left(D_V \frac{\partial T}{\partial z} \right) + \frac{S}{\rho_0 c_{pw}},$$

where x , y , and z are Cartesian coordinates (m), t is time (s), u , v and w are the three components of the water velocity (m/s), f is the Coriolis frequency in 1/s, T is the water temperature (K), ρ_0 is the water density (kg/m³), p is the pressure (Pa), ν_H and ν_V are the horizontal and vertical eddy viscosities (m²/s), D_H and D_V are the horizontal and vertical coefficients of eddy diffusivity of heat (m²/s), S is the source of heat per unit volume (W/m³) and c_{pw} is the water specific heat (J/K/kg). Model equations are precisely described (Deltares, 2014).

166 *Model set-up*

167 The surface of the numerical domain was created using a curvilinear grid composed of 591 cells of
168 about 1 km² area to fit the lake contour (Fig. 1). In the vertical direction, 100 Z-layers were used to fit
169 the bathymetry. Their thickness varies from 1 m at the surface to about 7 m at the bottom. Going
170 deeper, the thickness of two consecutive layers increases by a factor of 1.02. Based on these length
171 scales, the computational time step was set to 3 min to verify the Courant-Friedrichs-Lewy (CFL)
172 criterion and the background horizontal eddy viscosity and diffusivity was set to 100 m²/s. The k-ε
173 turbulence closure model was chosen to calculate the vertical eddy viscosity and diffusivity because it
174 has proven to perform well in stratified water (Burchard and Baumert, 1995). The explicit multi-
175 directional upwind (MDUE) scheme was selected for the spatial discretization of the horizontal
176 advection terms and the Van Leer-2 scheme was used for the transport equation. The wind drag
177 coefficient was set as a linear function of wind speed between 0.63 10⁻³ at 0 m/s and 7.23 10⁻³ at 100
178 m/s. Stanton and Dalton numbers were set at 1.3 10⁻³. The salinity was set constant at 0.15 ppt,
179 corresponding to the observed specific conductivity of about 300 μS/cm. The sediment transport and
180 resuspension in littoral zones and shallow areas was neglected because no measurements are available
181 to validate this part of the model and also because we did not refine the grid near the lake shore.

182 *Model input data*

183 Seven meteorological variables (air pressure, air temperature, cloud coverage, relative humidity,
184 incident solar radiation, wind speed and wind direction) coming from simulation results of the
185 Consortium for Small-scale Modeling (COSMO) two-dimensional atmospheric model were used in this
186 study (Fig. 3). The time step is 1 h and the spatial resolution is 1.5 km x 1.5 km. Hourly in situ
187 measurements of the discharge and the water temperature in the Rhône River at Porte De Scex, 5 km
188 upstream from the lake were also used (Fig. 3).

189 *Simulations*

190 The simulation starts on March 3, 2008, at midnight. A WT profile measured at SHL2 at this date was
191 used for initialization considering the whole lake water temperature as horizontally homogeneous. The
192 lake was also supposed to be at rest, without water currents. Five years were simulated, from 2008 to
193 2012. The simulation was stopped and restarted on January 1 of each year just to change the
194 transparency value. The average SDD value between May and September, the five months when the
195 solar radiation is the highest, was used (Wahl and Peeters, 2014). Values are presented in Table 2.
196 Simulation results were exported with a time-resolution of 1 h.

197 *Model validation*

198 The model performance was evaluated by comparing observed and simulated WT at SHL2 and GE3 for
199 the five simulated years. In this study, we focused on the water layer between the surface and 30 m
200 depth because this is where net photoautotrophic phytoplankton growth occurs. Simulated WT
201 profiles were systematically exported when in situ measurements were taken, at approximately
202 midday. The model validation was performed by calculating the mean absolute error (MAE), which
203 quantifies the error between simulation results and observations, defined by

$$204 \quad MAE = \frac{1}{n} \sum_{i=1}^n |T_{sim}(i) - T_{obs}(i)|$$

205 where T_{sim} and T_{obs} are respectively simulated and observed WT vectors whose length is n . One value
206 of MAE was calculated for each observation date by considering all the data between the surface and
207 30 m. One value of MAE was also computed for each depth and each year by considering all the data
208 of one year.

209 *Model analysis*

210 In this paper, we have chosen to focus on surface Chl-a structures that repeat from time to time. The
211 first structure was a phytoplankton patch with enhanced densities near the north-western shore of
212 the lake in summer. We focused on this particular structure which was observed on a MERIS image on
213 September 7, 2009 (Fig. 4). Accordingly, a first period, from August 31 to September 9, 2009, starting
214 with low and homogenous surface Chl-a was analyzed. The second structure depicts higher
215 phytoplankton abundance in early spring in a specific part of the lake, namely at the entrance of the
216 Rhône River (Kiefer et al., 2015) and it was observed on an image dated March 21, 2011 (Fig. 4).
217 Accordingly, a second period, from March 8 to 28, 2011, was analyzed. A third period of interest, from
218 February 24 to March 29, 2010, was chosen to be used as a counter-example for the 2nd structure.
219 During that period, environmental parameters allowed a homogenous development of phytoplankton
220 as clearly depicted by remote sensing in March 23, 2010. Changes in the lake thermal structure during
221 these three periods were analyzed based on hourly simulated WT profiles for three periods of interest
222 at four stations S1, S2, S3 and S4 (S2 and S4 correspond to SHL2 and GE3, respectively). Starting and
223 ending dates of the three periods corresponded to in situ sampling dates at the station SHL2.

224 Lake Analyzer is a numerical code that allows the calculation of several lake parameters using high
225 frequency data, it was used to calculate the mixed layer depth based on hourly simulation results (Read

et al., 2011). The mixed temperature differential parameter of Lake Analyzer was set to 0.01 °C. For the second and the third period of interest, Lake Analyzer was also used to calculate the buoyancy frequency, again based on hourly simulation results, which represents the local stability of the water column, N^2 , expressed in $1/s^2$ by
$$N^2 = \frac{g}{\rho} \frac{\partial \rho}{\partial z}$$

where g is the gravity (9.81 m/s^2), ρ is the water mass density (kg/m^3) and z is the vertical Cartesian coordinate (m).

Results

Model validation

The model was validated by comparing observed and simulated WT between the surface and 30 m depth at SHL2 (Fig. 5a) and at GE3 (Fig. 5b). Simulated WT were interpolated at observed depths and times. The 3D hydrodynamic model accurately reproduced the observations, in particular, the water column warming from the surface and the implementation of the thermal stratification during the summer. The MAE calculated for each observation date varies in a comparable way at SHL2 and GE3 ranging from 0.00 to 3.90 °C at SHL2 and 0.02 to 3.50 °C at GE3 (Fig. 6a). For both sampling stations, MAE values are smaller during winter and spring than during summer and autumn when the lake is stratified. The annual MAE calculated for each depth considering all the observation dates over the course of the year also varies comparably between SHL2 and GE3 with values comprised between 0.00 and 1.43 °C at SHL2 and between 0.22 and 1.89 °C at GE3 (Fig. 6b and Fig. 6c). The MAE is generally minimal at the surface and reaches a maximum at a depth located in the metalimnion near the thermocline, except for 2009 when the maximum value was found at the surface. In fact, the thermocline depth is better reproduced by the model for the year 2009. Below the metalimnion, the MAE decreases. The annual mean of the MAE is systematically lower at SHL2 than at GE3. Based on the MAE value, the best performances are achieved for the year 2012 followed by 2009, 2010, 2011 and 2008 (Table 3).

The comparison between measurements and simulations showed that the model is capable of reproducing the evolution of the lake thermal vertical structure on a smaller time-scale, especially for the three time-periods defined previously from surface Chl-a observations. During the first period from August 31 to September 9, 2009, the model satisfactorily reproduces the cooling of the water surface temperature and the deepening of the surface mixed layer at SHL2 (Fig. 7a). MAE values are presented in Table 4. For the period from February 24 to March 29, 2010, the model also correctly reproduces

the homogeneous onset of the thermal stratification (Fig. 7b). Finally, for the period from March 8 to 28, 2011, the model correctly predicted an early start of the stratification on March 28 at SHL2 while the lake was still not stratified on March 22 at GE3 (Fig. 7c). So, the model presents good results and can be safely used for the purpose of this study.

Lake thermal structure in summer 2009

From August 31 to September 2, 2009, simulation results predicted a homogeneous thermal stratification in the lake between the surface and 30 m depth, except at S1 near the main tributary entering the lake (Fig. 8b). In fact, the mixed layer depth was about 15 m at S1 and 10 m at S2, S3 and S4. On September 3, a wind event from west or southwesterly directions induced downwelling at S1 and upwelling at S4. This wind event continued on September 4 and increased, presenting wind speed values greater than 10 m/s (Fig. 8a). The minimum thickness of the surface mixed layer calculated by the model is 5.6 m at S4 and its maximum value is 25.3 m at S1 (Fig. 8c). Simulation results also predicted that water at 18.5 °C was brought up to the surface at the north-western shore (Fig. 9). This temperature value corresponded to a depth of about 15 m where the maximum of Chl-a was observed from in situ measurements at SHL2 on August 31 and September 9 (Fig. 10). Interestingly, the satellite image also shows high Chl-a concentration on September 7 along the north-western shore (Fig. 4).

Lake thermal structure in spring 2010

From February 24 to March 11, 2010, simulation results showed that thermal stratification did not occur between the surface and 30 m depth because several wind events (>5 m/s) from west or north-west and north or north-easterly directions prevented an increase in water column stability (Fig. 11). Conversely, the wind speed was lower between March 12 and 17 (<5 m/s) and daily stratification was predicted by the model. In fact, based on a stability criterion (thermal stratification was defined as $N^2 > 10^{-5} \text{ 1/s}^2$), thermal stratification started at the same time at S1, S2, S3 and S4 on March 16 due to the lower wind speed. Until March 23, the thermal stratification developed homogeneously across the four stations, no wind events were recorded that could have broken the stratification at any station. In comparison, the satellite image March 23 showed quite homogenous Chl-a concentrations at the whole lake scale (Fig. 4) and the maximum of Chl-a was observed from in situ measurements at SHL2 only on March 29 just below the surface (Fig. 10).

Lake thermal structure in spring 2011

From March 8 to 12, 2011, simulation results indicated that the lake was similarly mixed between the surface and 30 m depth at S1, S2, S3 and S4 when the wind speed did not exceed 5 m/s (Fig. 12). Between March 13 and 16, several strong wind events (>5 m/s) coming from the east or southeast regularly reduced the water column stability at S1 by breaking the small thermal stratification that had begun. On March 13, the buoyancy frequency at S1 passed from $6 \cdot 10^{-5}$ to $3 \cdot 10^{-6} \text{ 1/s}^2$ and continued to reach values below 10^{-5} 1/s^2 every day until March 16. Meanwhile, stability increased at S2, S3 and S4 where the wind speed was weaker allowing the development of thermal stratification. From March 17, onwards, the stability increased at S1 where the buoyancy frequency returned over 10^{-5} 1/s^2 due to a decrease in wind speed. On March 19, a strong wind event from north or northeasterly directions (10 m/s) mixed the water column at S3 and S4, and significantly decreased the water column stability at S2. At S4, the buoyancy frequency passed from $2 \cdot 10^{-4}$ to $3 \cdot 10^{-6} \text{ 1/s}^2$. The wind turned to the west, leaving S1 sheltered and S2 less exposed to the wind compared to S3 and S4. The north or northeast wind event continued after March 19 and prevented the thermal stratification restarting at S3 and S4. As a result, the lake thermal structure was not homogeneous throughout the lake, only S1 and S2 were stratified and S1 was more stratified than S2. In comparison, the satellite image on March 21 showed that algal development took place at S1 (Fig. 4) and the maximum of Chl-a was observed from in situ measurements at SHL2 only on March 28 just below the surface (Fig. 10).

Discussion

Model performance

At least five other 3D lake models including modeling of the water temperature were created using the open source Delft3D software: Lake Geneva in France/Switzerland (Razmi et al., 2017, 2014, 2013), Lake Constance in Switzerland/Germany/Austria (Wahl and Peeters, 2014), Lake Egirgir in Turkey (Kacikoc and Beyhan, 2014), Nam Theun 2 reservoir in Laos (Chanudet et al., 2012) and Lake Créteil in France (Soulignac et al., 2017). All these five models along with our proposed model, were validated using in situ measurements and proved to perform satisfactory, capable of accurately simulating the hydrodynamic and thermal structure of these lakes and proved to be ready to be used for research questions, for example climate research (Wahl and Peeters, 2014).

Razmi et al's model and ours were validated using vertical profiles of observed water temperature. They used two profiles at a single station in Vidy bay on August 5 and November 7, 2005, while we used monthly/bimonthly profiles at two stations, SHL2 and GE3, in the lake from 2008 to 2012. Model performances are similar during the studied periods. They found a RMSE from 0.90 to 2.00 °C and we obtained a MAE between 0.18 and 1.49 °C during spring and summer.

Early spring algal development onset in 2010 and 2011

In spring 2010, satellite surface Chl-a data showed that the onset of phytoplankton development was homogeneous in Lake Geneva. This is corroborated by the use of the 3D model which shows that the thermal structure of the lake was homogeneous too. By contrast in spring 2011, satellite images revealed heterogeneous Chl-a with a maximum recorded in the eastern part of the lake indicating that the onset of phytoplankton development occurred earlier at S1. Based on the satellite data, it was shown that this part of the lake regularly exhibits higher Chl-a concentrations in spring (Kiefer et al., 2015).

Given the mesotrophic status of the lake, in March, the euphotic layer receives an input of nutrients through winter mixing, bringing up nutrients from the bottom of the lake, which results in reactive phosphorus concentrations higher than 10 $\mu\text{g/l}$ in the euphotic zone. In Lake Geneva, phosphorus is not yet a limiting factor for phytoplankton growth at this time of the year because most species may be limited by phosphorus as concentration becomes less than 10 $\mu\text{g/l}$ (Sas, 1989) and severe reduction in algal growth may occur if soluble reactive phosphorus concentrations fall below 3 $\mu\text{g/l}$ (Grover, 1989; Suttle et al., 1988). Moreover, according to the conceptual model of the Plankton Ecology Group (PEG) (Sommer et al., 2012, 1986) and Reynolds (1997) in such deep lakes, light is the critical resource for phytoplankton growth in early spring. Observations confirm that phytoplankton developed in areas of Lake Geneva where our simulations indicated that the thermal stratification sets in earlier in a more sheltered area compared to the rest of the lake. Indeed, our results are coherent with the PEG model which states that thermal stratification triggers the algal development in spring in deep lakes due to enhanced light availability for phytoplankton growth resulting from restrictions on the mixing depth.

This concept has long been described as Sverdrup's critical mixing depth, i.e. phytoplankton is able to grow only if the mixing depth is less than a critical depth so that net photoautotrophic growth is possible (Sverdrup, 1953). However, this concept is not always in line with observations since phytoplankton blooms have been observed preceding the onset of stratification, when mixing is still unrestricted (Eilertsen, 1993). Huisman et al. (2009) added the concept of critical turbulence to the concept of critical mixing depth. In deep and relatively clear lakes, phytoplankton can maintain development, irrespective of mixing depth if their growth rate in the upper layer exceeds vertical mixing rates. The sheltered area in the eastern part of Lake Geneva may favor early bloom development following either one of these concepts, either by reducing mixing depth or by reducing turbulent mixing rates to below the respective critical values.

Upwelling event in summer 2009

Upwelling events were previously observed in some regions of Lake Geneva (Oesch et al., 2008) and more generally in large lakes (Plattner et al., 2006). When characterizing the thermal structure of Lake Geneva using the 3D model, we found that we could link satellite images and simulation results for the upwelling event of September 4, 2009. In situ measurements showed that phytoplankton developed at about 15 m depth at that time. We showed that surface Chl-a heterogeneities observed on September 7, 2009, are related to this upwelling event. The model suggests a displacement of deep phytoplankton to the surface and provides additional evidence of the role of upwelling on phytoplankton abundance heterogeneity in lakes (Cyr, 2017; Huang et al., 2014). At this stage, our model does not include nutrients or biology, so it cannot attest for an effective supply of nutrients to the upper waters that will stimulate algae productivity and phytoplankton growth. So, it remains unresolved whether the upwelling event indeed enhanced primary production and phytoplankton growth as is sometimes the case during upwelling events (Poschke et al., 2015).

However, this effective enhancement of algae production needs to be accurately tested because upwelling events are characterized as a “temporal displacement of near shore water masses which returned at the end of each event” (Haffner et al., 1984). Therefore, depending on the time scale, intensity and duration of the event, phytoplankton in the upper layer should receive little or no “benefit from the upwelled nutrient rich hypolimnetic waters” (Haffner et al., 1984). As a consequence, it is important to understand and assess when upwellings are efficient fertilizers of the euphotic zone as it has been recorded in various ecosystems (Planas and Paquet, 2016; Valipour et al., 2016). In addition, we should consider that special attention needs to be paid to the horizontal mixing occurring during and just after the upwelling event. Coupling our hydrodynamic model to a biological module should most likely allow us to estimate the impact of new nutrient availability in the surface waters. Such fertilization of the euphotic zone by nutrient enriched deep water might have an important role in the functioning of mesotrophic lakes. It is important to better assess if these hydrodynamic events can efficiently sustain primary production and how they impact the outcome of inter-specific competition within the phytoplankton community. Improving our understanding on the impact of these hydrodynamic events on phytoplankton communities, might help to understand usual patterns observed during re-oligotrophication of deep lakes such as changes in taxonomic composition (Jeppesen et al., 2005) or hysteresis in phytoplankton biomass (Tadonleke et al., 2009).

Furthermore, several undesirable phytoplankton species are known to develop at depth in alpine lakes. *Mougeotia gracillima* or *Planktothrix rubescens* develop and proliferate at 15-20 m depth near the thermocline in Lake Geneva (Jacquet et al., 2014b; Tapolczai et al., 2015). In the case of *M. gracillima* which is not toxic, an upwelling event should not cause any potential health risks for leisure activities

or production of drinking water. In contrast, if upwelling brings potentially toxic species such as *P. rubescens* to the lake surface where the contact with people is more intense than when it remains at greater depth, it may cause serious health issues (Ibelings et al., 2014). For that reason, in lakes subject to harmful algal bloom development in deeper layers, it should be relevant to improve our forecasting of upwelling events (Plattner et al., 2006) and we suggest the addition of additional in situ sampling of phytoplankton in these areas for identification of dominant species. 3D models and remote sensing products could help in identifying the areas where best to perform the sample collection.

Contribution of 3D models in the interpretation of spatial observations of Chl-a concentration from Satellite Data

Optical satellite remote sensing has been used to retrieve patterns of surface Chl-a concentration in lakes (Bresciani et al., 2011; Kiefer et al., 2015; Odermatt et al., 2012; Palmer et al., 2015). But this technique is not capable of detecting deep Chl-a concentration maxima which are common in deep lakes undergoing re-oligotrophication (Anneville and Lebouranger, 2001; Leach et al., 2018). This is a fundamental limitation of the use of satellite images in characterizing phytoplankton blooms in lakes. In order to improve Chl-a retrieval, 3D hydrodynamic models coupled to ecological models could be used to give information about the Chl-a structure in the vertical dimension which may vary between different portions of the lake.

Conclusion

A 3D hydrodynamic model of Lake Geneva was created. It is based on the Delft3D suite software and includes the main tributary (Rhône River) and 2D high-resolution meteorological forcing. It provides 3D maps of WT with a 1 h time step on a 1 km horizontal grid size and with a vertical resolution of 1 m near the surface to 7 m at the bottom of the lake. This model was validated using in situ measurements taken at two sampling stations in the lake over 5 years, from 2008 to 2012. Model performances were satisfactory, compared to the literature. Here, we have shown that such a model can be used to detail the lake thermal structure during two periods, one in spring and another in summer, when surface Chl-a heterogeneities were observed by satellite data. Both data comparisons performed well in providing explanations for horizontal heterogeneities in Chl-a abundances. For instance, we highlighted the important role of wind in determining surface phytoplankton abundance. A short and intense wind event in spring is able to create clear surface heterogeneities in phytoplankton distribution which continue through time. Also in summer, the role of the wind is very important. It can generate upwelling events and create surface Chl-a heterogeneities bringing potentially toxic species to the surface. If we look to the future, the validity of this approach and the possibility to export this

combination of techniques (3D model and remote sensing) to other study areas in the world could be considered a fruitful approach, as for example Pinardi et al. (2105) who effectively used the combination of a hydrodynamic model and of remote sensing derived products to assess potential algal bloom. Also, a coupled biological model to the hydrodynamic model could further help to understand better the phytoplankton dynamic and heterogeneities observed in Lake Geneva.

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Reference

Anneville, O. and Le Boulanger, C., 2001. Long-term changes in the vertical distribution of phytoplankton biomass and primary production in Lake Geneva: A response to the oligotrophication, *Atti Associazione Italiana Oceanologia Limnologia* 14, 25–35.

Arhonditsis, G.B., Winder, M., Brett, M.T., Schindler, D.E., 2004. Patterns and mechanisms of phytoplankton variability in Lake Washington (USA). *Water Res.* 38, 4013–4027. <https://doi.org/10.1016/j.watres.2004.06.030>

Bresciani, M., Stroppiana, D., Odermatt, D., Morabito, G., Giardino, C., 2011. Assessing remotely sensed chlorophyll-a for the implementation of the Water Framework Directive in European perialpine lakes. *Sci. Total Environ.* 409, 3083–3091. <https://doi.org/10.1016/j.scitotenv.2011.05.001>

Burchard, H., Baumert, H., 1995. On the performance of a mixed-layer model based on the κ - ϵ turbulence closure. *J. Geophys. Res.-Oceans* 100, 8523–8540. <https://doi.org/10.1029/94jc03229>

Chanudet, V., Fabre, V., van der Kaaij, T., 2012. Application of a three-dimensional hydrodynamic model to the Nam Theun 2 Reservoir (Lao PDR). *J. Great Lakes Res.* 38, 260–269. <https://doi.org/10.1016/j.jglr.2012.01.008>

443 Chen, Y.W., Fan, C.X., Teubner, K., Dokulil, M., 2003. Changes of nutrients and phytoplankton
444 chlorophyll-alpha in a large shallow lake, Taihu, China: an 8-year investigation. *Hydrobiologia* 506, 273–
445 279. <https://doi.org/10.1023/b:hydr.00000008604.09751.01>

446 Cyr, H., 2017. Winds and the distribution of nearshore phytoplankton in a stratified lake. *Water Res.*
447 122, 114–127. <https://doi.org/10.1016/j.watres.2017.05.066>

448 Deltares, 2014. Delft3D-FLOW, User Manual.

449 Eilertsen, H.C., 1993. Spring blooms and stratification. *Nature* 363, 24–24.
450 <https://doi.org/10.1038/363024a0>

451 European Commission, 2000. Directive 2000/60/EC of the European Parliament and of the Council of
452 23 October 2000 establishing a framework for community action in the field of water policy. Off. J. Eur.
453 Communities 2000.

454 Gons, H.J., Auer, M.T., Effler, S.W., 2008. MERIS satellite chlorophyll mapping of oligotrophic and
455 eutrophic waters in the Laurentian Great Lakes. *Remote Sens. Environ.* 112, 4098–4106.
456 <https://doi.org/10.1016/j.rse.2007.06.029>

457 Grover, J.P., 1989. Phosphorus-dependant growth kinetics of 11 species of freshwater algae. *Limnol.*
458 *Oceanogr.* 34, 341–348. <https://doi.org/10.4319/lo.1989.34.2.0341>

459 Haffner, G.D., Yallop, M.L., Hebert, P.D.N., Griffiths, M., 1984. Ecological significance of upwelling
460 events in Lake Ontario. *J. Gt. Lakes Res.* 10, 28–37. [https://doi.org/10.1016/s0380-1330\(84\)71804-1](https://doi.org/10.1016/s0380-1330(84)71804-1)

461 Huang, J.C., Gao, J.F., Hormann, G., Fohrer, N., 2014. Modeling the effects of environmental variables
462 on short-term spatial changes in phytoplankton biomass in a large shallow lake, Lake Taihu. *Environ.*
463 *Earth Sci.* 72, 3609–3621. <https://doi.org/10.1007/s12665-014-3272-z>

464 Huisman, J., van Oostveen, P., Weissing, F.J., 1999. Critical depth and critical turbulence: Two different
465 mechanisms for the development of phytoplankton blooms. *Limnol. Oceanogr.* 44, 1781–1787.
466 <https://doi.org/10.4319/lo.1999.44.7.1781>

467 Ibelings, B.W., Backer, L.C., Kardinaal, W.E.A., Chorus, I., 2014. Current approaches to cyanotoxin risk
468 assessment and risk management around the globe. *Harmful Algae* 40, 63–74.
469 <https://doi.org/10.1016/j.hal.2014.10.002>

470 Ibelings, B.W., Vonk, M., Los, H.F.J., van der Molen, D.T., Mooij, W.M., 2003. Fuzzy modeling of
 471 cyanobacterial surface waterblooms: Validation with NOAA-AVHRR satellite images. *Ecol. Appl.* 13,
 472 1456–1472. <https://doi.org/10.1890/01-5345>

473 Jacquet, S., Domaizon, I., Anneville, O., 2014a. The need for ecological monitoring of freshwaters in a
 474 changing world: a case study of Lakes Annecy, Bourget, and Geneva. *Environ. Monit. Assess.* 186,
 475 3455–3476. <https://doi.org/10.1007/s10661-014-3630-z>

476 Jacquet, S., Kerimoglu, O., Rimet, F., Paolini, G., Anneville, O., 2014b. Cyanobacterial bloom
 477 termination: the disappearance of *Planktothrix rubescens* from Lake Bourget (France) after
 478 restoration. *Freshw. Biol.* 59, 2472–2487. <https://doi.org/10.1111/fwb.12444>

479 Jeppesen, E., Sondergaard, M., Jensen, J.P., Havens, K.E., Anneville, O., Carvalho, L., Coveney, M.F.,
 480 Deneke, R., Dokulil, M.T., Foy, B., Gerdeaux, D., Hampton, S.E., Hilt, S., Kangur, K., Kohler, J., Lammens,
 481 E., Lauridsen, T.L., Manca, M., Miracle, M.R., Moss, B., Noges, P., Persson, G., Phillips, G., Portielje, R.,
 482 Schelske, C.L., Straile, D., Tatrai, I., Willen, E., Winder, M., 2005. Lake responses to reduced nutrient
 483 loading - an analysis of contemporary long-term data from 35 case studies. *Freshw. Biol.* 50, 1747–
 484 1771. <https://doi.org/10.1111/j.1365-2427.2005.01415.x>

485 Kacikoc, M., Beyhan, M., 2014. Hydrodynamic and Water Quality Modeling of Lake Egirdir. *Clean-Soil*
 486 *Air Water* 42, 1573–1582. <https://doi.org/10.1002/clen.201300455>

487 Kauer, T., Kutser, T., Arst, H., Danckaert, T., Noges, T., 2015. Modelling primary production in shallow
 488 well mixed lakes based on MERIS satellite data. *Remote Sens. Environ.* 163, 253–261.
 489 <https://doi.org/10.1016/j.rse.2015.03.023>

490 Kiefer, I., Odermatt, D., Anneville, O., Wuest, A., Bouffard, D., 2015. Application of remote sensing for
 491 the optimization of in-situ sampling for monitoring of phytoplankton abundance in a large lake. *Sci.*
 492 *Total Environ.* 527, 493–506. <https://doi.org/10.1016/j.scitotenv.2015.05.011>

493 Leach, T.H., Beisner, B.E., Carey, C.C., Pernica, P., Rose, K.C., Huot, Y., Brentrup, J.A., Domaizon, I.,
 494 Grossart, H.-P., Ibelings, B.W., Jacquet, S., Kelly, P.T., Rusak, J.A., Stockwell, J.D., Straile, D., Verburg,
 495 P., 2018. Patterns and drivers of deep chlorophyll maxima structure in 100 lakes: The relative
 496 importance of light and thermal stratification. *Limnol. Oceanogr.* 63, 628–646.
 497 <https://doi.org/10.1002/lno.10656>

498 Lemmin, U., 1995. Limnologie physique, in: Pourriot, R. and Meybeck, M. (Eds.), Limnologie générale.
 499 Masson, Paris, pp. 60–114.

500 Leoni, B., Marti, C.L., Imberger, J., Garibaldi, L., 2014. Summer spatial variations in phytoplankton
 501 composition and biomass in surface waters of a warm-temperate, deep, oligoholomictic lake: Lake
 502 Iseo, Italy. *Inland Waters* 4, 303–310. <https://doi.org/10.5268/iw-4.3.569>

503 Li, Z.J., Chen, Q.W., Xu, Q., 2015. Modeling algae dynamics in Meiliang Bay of Taihu Lake and parameter
 504 sensitivity analysis. *J. Hydro-Environ. Res.* 9, 216–225. <https://doi.org/10.1016/j.jher.2014.10.001>

505 McCombs, M.P., Mulligan, R.P., Boegman, L., 2014. Offshore wind farm impacts on surface waves and
 506 circulation in Eastern Lake Ontario. *Coast. Eng.* 93, 32–39.
 507 <https://doi.org/10.1016/j.coastaleng.2014.08.001>

508 Moreno-Ostos, E., da Silva, S.L.R., de Vicente, I., Cruz-Pizarro, L., 2007. Interannual and between-site
 509 variability in the occurrence of clear water phases in two shallow Mediterranean lakes. *Aquat. Ecol.*
 510 41, 285–297. <https://doi.org/10.1007/s10452-006-9072-0>

511 Odermatt, D., Pomati, F., Pitarch, J., Carpenter, J., Kawka, M., Schaepman, M., Wuest, A., 2012. MERIS
 512 observations of phytoplankton blooms in a stratified eutrophic lake. *Remote Sens. Environ.* 126, 232–
 513 239. <https://doi.org/10.1016/j.rse.2012.08.031>

514 Oesch, D., Jaquet, J.M., Klaus, R., Schenker, P., 2008. Multi-scale thermal pattern monitoring of a large
 515 lake (Lake Geneva) using a multi-sensor approach. *Int. J. Remote Sens.* 29, 5785–5808.
 516 <https://doi.org/10.1080/01431160802132786>

517 Palmer, S.C.J., Odermatt, D., Hunter, P.D., Brockmann, C., Presing, M., Balzter, H., Toth, V.R., 2015.
 518 Satellite remote sensing of phytoplankton phenology in Lake Balaton using 10 years of MERIS
 519 observations. *Remote Sens. Environ.* 158, 441–452. <https://doi.org/10.1016/j.rse.2014.11.021>

520 Pelechaty, M., Owsianny, P.M., 2003. Horizontal distribution of phytoplankton as related to the spatial
 521 heterogeneity of a lake - a case study from two lakes of the Wielkopolski National Park (western
 522 Poland). *Hydrobiologia* 510, 195–205. <https://doi.org/10.1023/B:HYDR.0000008644.67963.c4>

523 Pinardi, M., Fenocchi, A., Giardino, C., Sibilla, S., Bartoli, M., & Bresciani, M., 2015. Assessing potential
 524 algal blooms in a shallow fluvial lake by combining hydrodynamic modelling and remote-sensed
 525 images. *Water* 7(5), 1921–1942. <https://doi.org/10.3390/w7051921>

526 Planas, D., Paquet, S., 2016. Importance of climate change-physical forcing on the increase of
 527 cyanobacterial blooms in a small, stratified lake. *J. Limnol.* 75, 201–214.
 528 <https://doi.org/10.4081/jlimnol.2016.1371>

529 Plattner, S., Mason, D.M., Leshkevich, G.A., Schwab, D.J., Rutherford, E.S., 2006. Classifying and
 530 forecasting coastal upwellings in Lake Michigan using satellite derived temperature images and buoy
 531 data. *J. Gt. Lakes Res.* 32, 63–76. [https://doi.org/10.3394/0380-1330\(2006\)32\[63:cafcui\]2.0.co;2](https://doi.org/10.3394/0380-1330(2006)32[63:cafcui]2.0.co;2)

532 Pomati, F., Jokela, J., Simona, M., Veronesi, M., Ibelings, B.W., 2011. An Automated Platform for
 533 Phytoplankton Ecology and Aquatic Ecosystem Monitoring. *Environ. Sci. Technol.* 45, 9658–9665.
 534 <https://doi.org/10.1021/es201934n>

535 Poschke, F., Lewandowski, J., Engelhardt, C., Preuss, K., Oczipka, M., Ruhtz, T., Kirillin, G., 2015.
 536 Upwelling of deep water during thermal stratification onset-A major mechanism of vertical transport
 537 in small temperate lakes in spring? *Water Resour. Res.* 51, 9612–9627.
 538 <https://doi.org/10.1002/2015wr017579>

539 Razmi, A.M., Barry, D.A., Bakhtyar, R., Le Dantec, N., Dastgheib, A., Lemmin, U., Wuest, A., 2013.
 540 Current variability in a wide and open lacustrine embayment in Lake Geneva (Switzerland). *J. Gt. Lakes*
 541 *Res.* 39, 455–465. <https://doi.org/10.1016/j.jglr.2013.06.011>

542 Razmi, A.M., Barry, D.A., Lemmin, U., Bonvin, F., Kohn, T., Bakhtyar, R., 2014. Direct effects of dominant
 543 winds on residence and travel times in the wide and open lacustrine embayment: Vidy Bay (Lake
 544 Geneva, Switzerland). *Aquat. Sci.* 76, S59–S71. <https://doi.org/10.1007/s00027-013-0321-8>

545 Razmi, A.M., Lemmin, U., Bouffard, D., Wuest, A., Uittenbogaard, R.E., Barry, D.A., 2017. Gyre
 546 formation in open and deep lacustrine embayments: the example of Lake Geneva, Switzerland.
 547 *Environ. Fluid Mech.* 17, 415–428. <https://doi.org/10.1007/s10652-016-9494-8>

548 Read, J.S., Hamilton, D.P., Jones, I.D., Muraoka, K., Winslow, L.A., Kroiss, R., Wu, C.H., Gaiser, E., 2011.
 549 Derivation of lake mixing and stratification indices from high-resolution lake buoy data. *Environ.*
 550 *Model. Softw.* 26, 1325–1336. <https://doi.org/10.1016/j.envsoft.2011.05.006>

551 Reynolds, C.S., 1997. Vegetation process in the pelagic: a model for ecosystem theory. In Kinne, O.
 552 (ed.), *Excellence in Ecology*. ECI, Oldendorf.

553 Sas, H., 1989. Lake restoration by reduction of nutrient loading: Expectations, experiences,
554 extrapolations. Academia Verlag Richarz, St. Augustin.

555 Schroeder, T., Behnert, I., Schaale, M., Fischer, J., Doerffer, R., 2007. Atmospheric correction algorithm
556 for MERIS above case-2 waters. *Int. J. Remote Sens.* 28, 1469–1486.
557 <https://doi.org/10.1080/01431160600962574>

558 Sommer, U., Adrian, R., Domis, L.D., Elser, J.J., Gaedke, U., Ibelings, B., Jeppesen, E., Lurling, M.,
559 Molinero, J.C., Mooij, W.M., van Donk, E., Winder, M., 2012. Beyond the Plankton Ecology Group (PEG)
560 Model: Mechanisms Driving Plankton Succession. *Annu. Rev. Ecol. Evol. Syst.* Vol 43 43, 429–448.
561 <https://doi.org/10.1146/annurev-ecolsys-110411-160251>

562 Sommer, U., Gliwicz, Z.M., Lampert, W., Duncan, A., 1986. The PEG-model of seasonal succession of
563 planktonic events in fresh waters. *Arch. Hydrobiol.* 106, 433–471.

564 Soullignac, F., Vincon-Leite, B., Lemaire, B.J., Martins, J.R.S., Bonhomme, C., Dubois, P., Mezemate, Y.,
565 Tchiguirinskaia, I., Schertzer, D., Tassin, B., 2017. Performance Assessment of a 3D Hydrodynamic
566 Model Using High Temporal Resolution Measurements in a Shallow Urban Lake. *Environ. Model.*
567 *Assess.* 22, 309–322. <https://doi.org/10.1007/s10666-017-9548-4>

568 Stewart, T.J., Rudstam, L., Watkins, J., Johnson, T.B., Weidel, B., Koops, M.A., 2016. Research needs to
569 better understand Lake Ontario ecosystem function: A workshop summary. *J. Gt. Lakes Res.* 42, 1–5.
570 <https://doi.org/10.1016/j.jglr.2015.10.017>

571 Suttle, C.A., Stockner, J.G., Shortreed, K.S., Harrison, P.J., 1988. Time-courses of size-fractionated
572 phosphote uptake: are larger cells better competitors for pulse of phosphate than smaller cells.
573 *Oecologia* 74, 571–576. <https://doi.org/10.1007/bf00380055>

574 Sverdrup, H.U., 1953. On conditions for the vernal blooming of phytoplankton. *ICES Journal of Marine*
575 *Sci.* 18, 287–295. <https://doi.org/10.1093/icesjms/18.3.287>

576 Tadonleke, R.D., Lazzarotto, J., Anneville, O., Druart, J.C., 2009. Phytoplankton productivity increased
577 in Lake Geneva despite phosphorus loading reduction. *J. Plankton Res.* 31, 1179–1194.
578 <https://doi.org/10.1093/plankt/fbp063>

579 Tapolczai, K., Anneville, O., Padisak, J., Salmaso, N., Morabito, G., Zohary, T., Tadonleke, R.D., Rimet,
 580 F., 2015. Occurrence and mass development of *Mougeotia* spp. (Zygnemataceae) in large, deep lakes.
 581 *Hydrobiologia* 745, 17–29. <https://doi.org/10.1007/s10750-014-2086-z>

582 Valipour, R., Leon, L.F., Depew, D., Dove, A., Rao, Y.R., 2016. High-resolution modeling for development
 583 of nearshore ecosystem objectives in eastern Lake Erie. *J. Gt. Lakes Res.* 42, 1241–1251.
 584 <https://doi.org/10.1016/j.jglr.2016.08.011>

585 Viljanen, M., Holopainen, A.L., Rahkola-Sorsa, M., Avinsky, V., Ruuska, M., Leppanen, S., Rasmus, K.,
 586 Voutilainen, A., 2009. Temporal and spatial heterogeneity of pelagic plankton in Lake Pyhaselka,
 587 Finland. *Boreal Environ. Res.* 14, 903–913.

588 Wahl, B., Peeters, F., 2014. Effect of climatic changes on stratification and deep-water renewal in Lake
 589 Constance assessed by sensitivity studies with a 3D hydrodynamic model. *Limnol. Oceanogr.* 59, 1035–
 590 1052. <https://doi.org/10.4319/lo.2014.59.3.1035>

591 Xu, F.L., Tao, S., Dawson, R.W., Li, P.G., Cao, J., 2001. Lake ecosystem health assessment: Indicators
 592 and methods. *Water Res.* 35, 3157–3167. [https://doi.org/10.1016/s0043-1354\(01\)00040-9](https://doi.org/10.1016/s0043-1354(01)00040-9)

593 **Tables**

594 Table 1: Lake Geneva characteristics

Characteristic	Value
Latitude	N 46° 27'
Longitude	E 6° 32'
Elevation	372 m
Mean depth	153 m
Max depth	309 m
Surface area	580 km ²
Watershed area	7475 km ²

595 Table 2: Model input data Secchi disk depth (SDD) from 2008 to 2012

Year	SDD (m)
2008	6.1
2009	6.4

2010	6.1
2011	6.0
2012	4.0

Table 3: Annual mean values of the mean absolute error between the surface and 30 m depth for the two monitoring stations, SHL2 and GE3, from 2008 to 2012

	SHL2	GE3
2008	1.07	1.30
2009	0.79	0.97
2010	0.80	1.29
2011	1.07	1.20
2012	0.72	0.80

Table 4: Mean absolute error values between the surface and 30 m depth at the two monitoring stations, SHL2 and GE3, during the three periods analyzed (NA: not available)

	SHL2	GE3
31/08/2009	1.27	NA
09/09/2009	1.49	NA
24/02/2010	0.52	NA
17/03/2010	0.57	NA
23/03/2010	NA	0.53
29/03/2010	0.54	NA
08/03/2011	0.57	NA
20/03/2011	NA	0.18
28/03/2011	0.54	NA

Figure captions

Fig. 1: Lake Geneva contour, isodepths (100, 200 and 300 m), numerical domain (curvilinear grids), location of the main tributary inflow and outflow (Rhône River) and location of the four sites where simulation outputs are analyzed (S1, S2 (SHL2), S3, S4 (GE3))

Fig. 2: Data availability

605 Fig.3: Model input meteorological data at the monitoring station SHL2 (air pressure (AP), air
606 temperature (AT), cloud coverage (CC), relative humidity (RH), incident solar radiation (SW), wind
607 speed (U10) and wind direction $\alpha 10$) and hourly flow rate (Qin) and water temperature (Tin) of the
608 Rhône River)

609 Fig. 4: Satellite chlorophyll-a concentration (Chl-a) data

610 Fig. 5: Comparison between observed and simulated water temperature (WT) at SHL2 (a) and GE3 (b)
611 using contour plots

612 Fig. 6: a) Times series of mean absolute error (MAE) between the surface and 30 m depth, b) Vertical
613 profiles of annual MAE

614 Fig. 7: Comparison between observed and simulated vertical profiles of WT at the two monitoring
615 stations, SHL2 and GE3, during the three periods analyzed

616 Fig. 8: First period of interest analyzed in summer 2009, a) Times series of wind speed (U10) and
617 direction ($\alpha 10$), b) Contour plots of simulated water temperature (WT) at the four stations, S1, S2, S3
618 and S4, and c) Comparison of mixed layer depths (metaT) across the lake

619 Fig. 9: Simulated surface water temperature (WT) on September 4, 2009, every two hours during the
620 first period of interest analyzed

621 Fig. 10: In situ Chl-a measurements at SHL2 monitoring station

622 Fig. 11: Second period of interest analyzed in spring 2010, a) Times series of wind speed (U10) and
623 direction ($\alpha 10$), b) Contour plots of simulated water temperature (WT) at the four stations, S1, S2, S3
624 and S4, and c) Comparison of buoyancy frequency (N^2) across the lake

625 Fig. 12: Third period of interest analyzed in spring 2011, a) Times series of wind speed (U10) and
626 direction ($\alpha 10$), b) Contour plots of simulated water temperature (WT) at the four stations, S1, S2, S3
627 and S4, and c) Comparison of buoyancy frequency (N^2) across the lake

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