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© *O. P. Savchuk*[1]*, *A. V. Isaev*[2], *N. N. Filatov*[3], 2022

[1]Baltic Nest Institute, Stockholm University Baltic Sea Centre, Stockholm, 10691, Sweden
[2]Shirshov Institute of Oceanology, Russian Academy of Sciences, 117997, Nahimovsky Pr., 36, Moscow, Russia
[3]Northern Water Problems Institute, Karelian Research Center, Russian Academy of Sciences,
185030, Pr. Al. Nevskogo, 50, Petrozavodsk, Russia
*E-mail: oleg.savchuk@su.se

THREE-DIMENSIONAL HINDCAST OF NITROGEN AND PHOSPHORUS BIOGEOCHEMICAL DYNAMICS IN LAKE ONEGO ECOSYSTEM, 1985–2015. PART II: SEASONAL DYNAMICS AND SPATIAL FEATURES; INTEGRAL FLUXES

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Abstract

A three-dimensional coupled hydrodynamical biogeochemical model of the nitrogen and phosphorus cycles has been used for a long-term reanalysis of the Lake Onego ecosystem. The comparison between simulation and sparse irregular observations, presented in the first part of this paper, demonstrated plausibility of the reconstructed temporal and spatial features of biogeochemical dynamics at a long-term scale, while seasonal dynamics of variables and fluxes are presented here. As new regional phenological knowledge, the reanalysis quantifies that the spring phytoplankton bloom, previously overlooked, reaches a maximum of 500 ± ± 128 mg C m^{-2} d^{-1} in May, contributes to approximately half of the lake's annual primary production of 17.0–20.6 g C m^{-2} yr^{-1}, and is triggered by increasing light availability rather than by an insignificant rise in water temperature. Coherent nutrient budgets provide reliable estimates of phosphorus and nitrogen residence times of 47 and 17 years, respectively. The shorter nitrogen residence time is explained by sediment denitrification, which in Lake Onego removes over 90 % of the bioavailable nitrogen input, but is often ignored in studies of other large lakes. An overall assessment of the model performance allows us considering the model a necessary and reliable tool for scenario simulations of possible changes in the Lake Onego ecosystem at the requested spatial and temporal scales.

Keywords: Lake Onego, nitrogen, phosphorus, biogeochemical cycles, mathematical modeling

© *О. П. Савчук*[1]*, *А. В. Исаев*[2], *Н. Н. Филатов*[3], 2022

[1]Балтик Нест Институт Стокгольмского университета, г. Стокгольм, 10691, Швеция
[2]Институт океанологии им. П.П. Ширшова РАН, 117997, Нахимовский пр., д. 36, г. Москва, Россия
[3]Институт водных проблем Севера, Карельский научный центр РАН, 185030, г. Петрозаводск, пр. Александра Невского, д. 50, Республика Карелия, Россия
*E-mail: oleg.savchuk@su.se

ТРЕХМЕРНАЯ РЕТРОСПЕКТИВНАЯ ОЦЕНКА БИОГЕОХИМИЧЕСКОЙ ДИНАМИКИ АЗОТА И ФОСФОРА В ЭКОСИСТЕМЕ ОНЕЖСКОГО ОЗЕРА ЗА ПЕРИОД С 1985 ПО 2015 ГГ. ЧАСТЬ II: СЕЗОННАЯ ДИНАМИКА И ПРОСТРАНСТВЕННЫЕ ОСОБЕННОСТИ; ИНТЕГРАЛЬНЫЕ ПОТОКИ

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Аннотация

Для многолетнего реанализа экосистемы Онежского озера была использована трехмерная объединенная гидродинамическая биогеохимическая модель круговоротов азота и фосфора. Сопоставление моделирования и разрозненных нерегулярных наблюдений, представленное в первой части статьи, продемонстрировало достоверность восстановленных временных и пространственных особенностей биогеохимической динамики в многолетнем масштабе. В данной

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работе представлена сезонная динамика компонентов экосистемы и биогеохимических потоков. В качестве новой региональной фенологической информации дана количественная оценка весеннего цветения фитопланктона, которое ранее упускалось из виду, но достигает максимума 500 ± 128 мгС $м^{-2}$ $сут^{-1}$ в мае, что составляет примерно половину годовой первичной продукции озера в размере 17,0–20,6. гС $м^{-2}$ $год^{-1}$, и вызывается увеличением доступности света, а не незначительным повышением температуры воды. Когерентные балансы питательных веществ обеспечивают надежные оценки времени пребывания фосфора и азота в 47 и 17 лет соответственно. Более короткое время пребывания азота объясняется денитрификацией отложений, которая в Онежском озере удаляет более 90 % биодоступного поступления азота, но часто игнорируется при исследованиях других крупных озер. Общая оценка работоспособности модели позволяет считать ее необходимым и надежным инструментом для сценарного моделирования возможных изменений экосистемы Онежского озера в требуемых пространственных и временных масштабах.

Ключевые слова: Онежское озеро, азот, фосфор, биогеохимические циклы, математическое моделирование

1. Introduction

Development of social responses to the current projections of climate change, human impacts, and their interactions made for the entire Baltic Sea Region [1, 2] require a reliable tool that could be conveniently used for downscaling and appropriate localisation of such projections for the Lake Onego ecosystem. An ultimate tool for performing such highly sophisticated tasks is an ecosystem modelling [3–6], including modelling of Ladoga and Onego lakes [7–10]. The necessary model has recently been developed and its plausible performance at a long-term large-scale was presented in the first part of this paper [11]. Here, we continue the presentation of model performance at the seasonal scales as well as analyse the biogeochemical fluxes as the most important driving force behind the dynamics of variables.

2. Seasonal dynamics

Here, we begin with presenting long-term average seasonal dynamics (cf. Fig. 8 in [11]) before analysing its mechanisms. As there is no available data on the phenological phase of the spring phytoplankton bloom in Lake Onego, we present this biogeochemically important phenomenon in more detail for the first time.

The maximum concentration of inorganic nutrients is reached when the winter accumulation due to pelagic and sediment remineralization is interrupted because of increasing nutrient uptake by developing phytoplankton. Thus, the date of maximum inorganic nutrients can be considered the onset of spring blooming, which, in the model, begins at the end of April with half-month interannual fluctuations (Table 1). Within these fluctuations, there is a tendency for an earlier spring onset, from the beginning of May to the end of April (cf. Fig. 7 in [11]). For phytoplankton primary production, dominated in spring by diatoms, it takes an average of 1 month to reach its maximum, commencing over the years as early as May 3 and as late as June 13 in some years, without any long-term trend.

Although a spring bloom phase is typical in boreal and arctic lakes phenology [12–17], there is almost no information on daily spring PP values measured in limnological conditions, similar to that of the boreal oligotrophic Lake Onego, situated between 61° N and 63° N. In Lake Baikal, areal primary production was measured as 800 ± 310 mg C m^{-2} d^{-1}under exceptionally transparent ice [18]. In Lake Superior, a PP rate of 220 mg C m^{-2} d^{-1} was measured on April 30, 2008 [19], while rates of 150 mg C m^{-2} d^{-1} and 200 mg C m^{-2} d^{-1} were reported from ice-free April 1999 and partly icy June in 2000 [20]. These measurements are extremely similar to the spring maxima simulated with a medium-complexity ecosystem model for 1997–2001, reaching up to 200 mg C m^{-2} d^{-1} [21]. As can only be expected, Lake Onego's spring maximum PP rates are approximately twice of the rates in Lake Superior, where median TP and DIP concentrations were less than 3 mg P m^{-3} and 0.7 mg P m^{-3} [22], that is, less than a third of Lake Onego's winter maximum stocks, providing for a much higher autochthonous production of organic matter

Table 1

Simulated spring maxima of winter nutrient surface accumulation (mg P (N) m^{-3}), phytoplankton primary production (PP, mg C m^{-2} d^{-1}), and biomass (Phyto, g wet weight m^{-3}) accompanied by the Gregorian day of year of its commencement (mean ± SD) with the range of its occurrence

	DIP	TP	DIN	TN	PP	Phyto
Maximum	6.0 ± 0.4	11.4 ± 0.6	230 ± 34	710 ± 74	500 ± 128	1.4 ± 0.3
Min/max	5.0/6.8	10.2/12.6	164/279	574/808	288/723	0.8/1.9
Day of year	118 ± 12	124 ± 12	116 ± 11	121 ± 11	149 ± 12	139 ± 9
Date range	Mar 27–May 15	Apr 2–May 21	Mar 28–May 14	Mar 31–May 19	May 3–Jun 13	May 3–Jun 5

(cf. Fig. 8, *a* and Fig. 9, *d* in [11]; Table 1). Higher spring PP rates of up to 1200 mg C m^{-2} d^{-1} were measured in 1985—1987 in three small Northern Wisconsin lakes located at 46° N and having comparable to Lake Onego spring TP concentrations [23]. Similarly, high spring rates of 800—1200 mg C m^{-2} d^{-1} were measured in the offshore region of south-eastern Lake Michigan in the 1980s and the 1990s [24].

After the spring bloom, the simulated ecosystem segued into the summer phase (see Fig. 9, *d*, *e* in [11], and Fig. 1 and Fig. 2 below), characterized by progressively decreasing phytoplankton biomass to levels of approximately 0.1 and 0.4 g ww m^{-3} in the open waters and the major bays, respectively. Phytoplankton PP in these regions remained in a quasi-steady state, at less than 100 and 200—300 mg C m^{-2} d^{-1} in the open waters and major bays, respectively (cf. Table 1 in [11]). During summer, the simulated open-lake average diatom biomass of 0.1 g ww m^{-3} still dominated the phytoplankton community. The concurrently developing simulated non-diatom complex reached its maximum biomass of 0.01 g ww m^{-3} in July — August. Unfortunately, the paucity and irregularity of available data hamper an appropriate model-data comparison. For instance, the wide ranges of phytoplankton biomass in Central and Big Onego during summer (July — October) of 1989—2006 are based on only 32 and 34 measurements of diatom and non-diatom biomass, respectively [25]. The median ± the standard error of the median, estimated from these scarce data are 0.42 ± 0.108 g ww m^{-3} and 0.027 ± 0.012g ww m^{-3} for the diatom and non-diatom biomass, respectively (Table 1 in [25]).

Organic matter produced by phytoplankton accumulated in the water column to levels of up to 5 mg P m^{-3} (compare the difference between DIP and TP in Fig. 8, *c* in [11]). Its particulate fraction (detritus) exceeded 1—2 mg P m^{-3} in the epilimnion and, together with phytoplankton, was grazed by zooplankton, whose biomass reached its maximum of 0.1—0.2 g ww m^{-3} in July — August. The average value of zooplankton biomass measured during the vegetation period was 0.1—0.33 g ww m^{-3} [8]. Unconsumed and non-mineralized detritus sediments out on the lake bottom, where it is partly buried and mineralized generating characteristic seasonal dynamics (cf. Fig. 8, *f* in [11]). With a sediment weight C: N ratio of approximately 10 [26, 27], the amplitude of seasonal variations of 1 g N m^{-2} corresponds to organic carbon seasonal variations in the sediments of approximately 10 g C m^{-2}. Primary production during autumn diatom blooming and phytoplankton biomass was simulated up to 130 mg C m^{-2} d^{-1} and 0.2 g ww m^{-3}, respectively, which constitutes triple that reported as 40 mg C m^{-2} d^{-1} and quarter that reported as 0.8 g ww m^{-3} [25].

Regarding phenological generalization [25, 28], it is worth noting that a neglect of the spring phytoplankton bloom phenomenon as well as the normalization by the maximum value measurements available only from the post-bloom “summer window”, which is rather typical in lake research [13], has resulted in a number of misleading implications. Here, we amend such implications with the following conclusions: a) the seasonal maximum of daily PP and the greatest contribution to annual PP occurred during spring, not summer; b) the initiation of the vegetational season was due to increasing light availability, with temperature dynamics playing a later role, due to thermal convection and augmented nutrient regeneration (see below); and c) the spring bloom was produced by diatoms, which contributed most also to the summer both biomass (Fig. 1) and PP in all regions except for the Kondopoga and Zaonegskiy bays, where their contributions were approximately the same as that of non-diatoms (not shown).

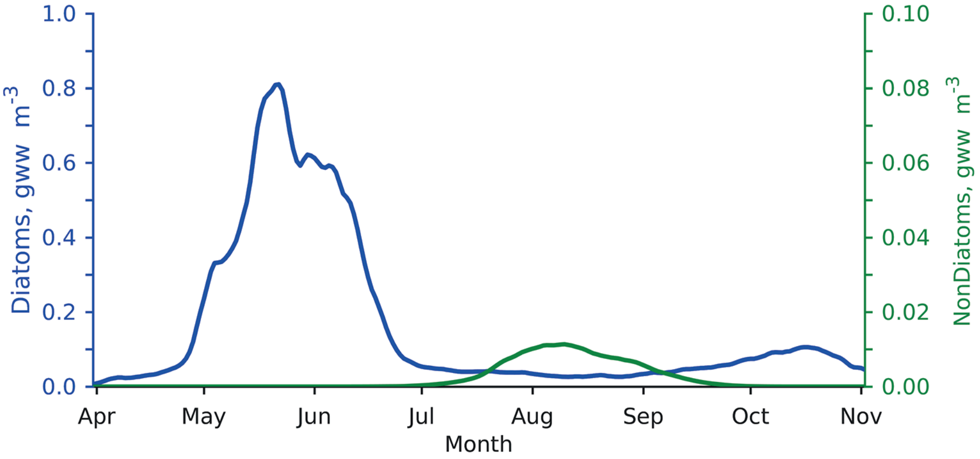

Fig. 1. Long-term average (1985—2015) of the simulated seasonal dynamics of diatom and non-diatom biomass (note ten-fold difference in scale) averaged over surface layer of four open water limnic regions (South Onego, Central Onego, Big Onego, and Small Onego, see also Fig. 2 in [11])

The mechanisms of seasonal dynamics in boreal lake ecosystems are well known, although the under-ice and melting-ice phases have often been overlooked and understudied [13, 29]. In the model developed in this study, seasonal ecosystem dynamics were determined by a close interaction between physical phenomena including transports, and biogeochemical processes (Fig. 2). Under the condition of reverse temperature stratification (Fig. 2, *a*), hampering the downward mixing of phytoplankton cells, winter accumulation of phosphates in the water column, occurring mostly owing to sediment release of mineralization products (Fig. 2, *b*), was interrupted by a mounting phosphate uptake by developing phytoplankton. The increasing phytoplankton growth rate was determined by the rise in light availability occurring in the model with the ice melt. Phytoplankton PP and biomass quickly reached their maxima (Fig. 2, *c*, see also Table 1) and continued to develop with the support of phosphates brought upwards by total lake turnover when water temperature reached its ubiquitous value of 4 °C. Later on, when the surface layer was depleted of DIP, the phytoplankton continued autotrophic activity in the deeper water layer under the thermocline [19, 30, 31], where light needed for photosynthesis was still sufficient. DIP also became available due to upward transport from the deeper layers, where DIP had been accumulating owing to organic matter mineralization in the water body

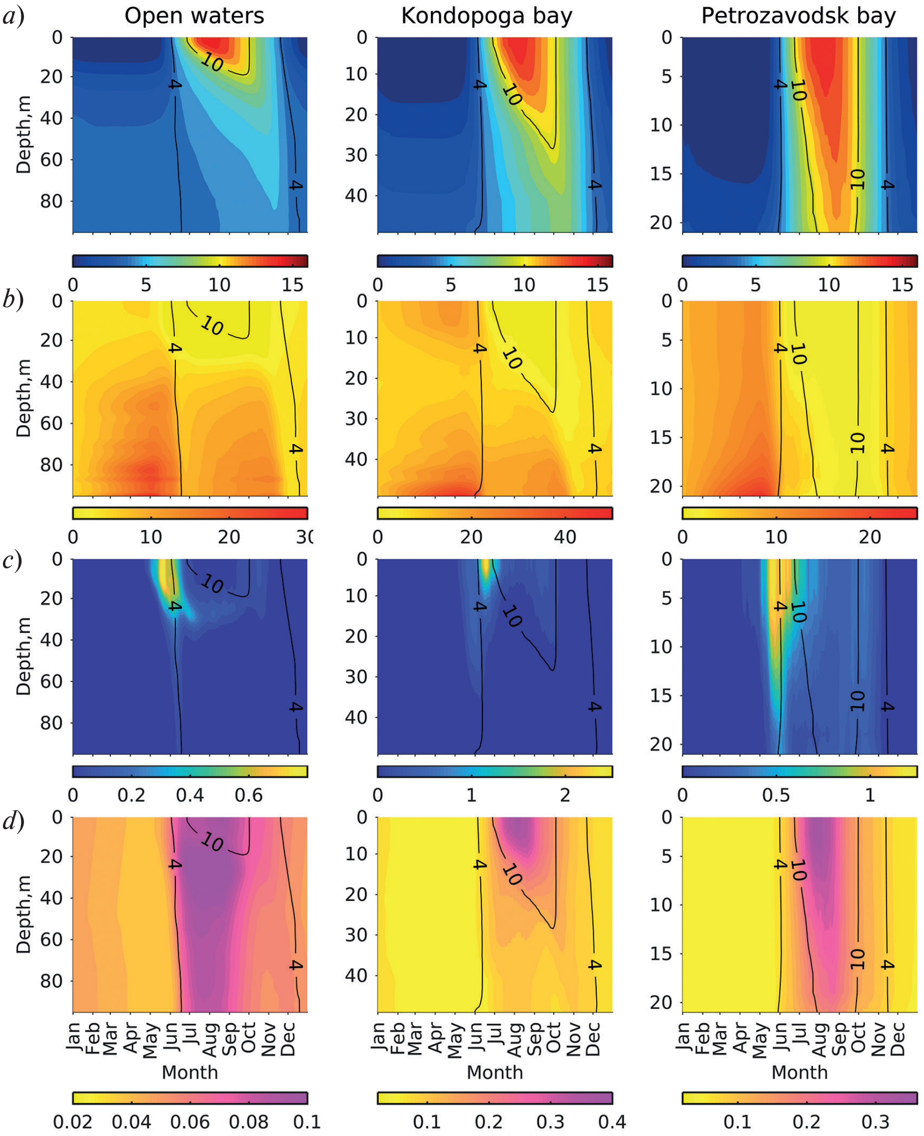

Fig. 2. Simulated long-term average (1985–2015) time-depth seasonal dynamics of water temperature, °C (*a*); DIP, mg P m^{-3} (*b*); phytoplankton biomass, g ww m^{-3} (*c*); and zooplankton biomass g ww m^{-3} (*d*) in openwaters (South, Central, Big, and Small Onego) shown in left panel, Kondopoga (middle panel), and Petrozavodsk (right panel) bays, see also Fig. 2 in [11]). Contour plots are overlaid with isotherms of 4 °C (temperature of maximal water density) and 10 °C (delimiting "biological summer"). Note differences in depth and colour palette scales

and sediments. In the shallower Kondopoga and, especially Petrozavodsk bays the direct support of the primary production by the sediment mineralization is even more pronounced (Fig. 2, *b* and *c*). Organic matter produced by autotrophs and distributed through the water column as both live cells and detritus feed zooplankton, allowing them to reach their maxima in August (Fig. 2, *d*). Vertical water convection associated with autumn cooling brought up enough phosphates to support a minor autumn bloom (Fig. 2, *b*, *c*).

As organic matter oxidized via limnetic and sediment biochemical mineralization as well as zooplankton catabolism consumed oxygen, the dynamics of its concentration in the hypolimnion (not shown) were reciprocal to the dynamics of phosphate as a product of organic phosphorus oxidation (Fig. 2, *b*). In deep water layers, the winter maximum oxygen reserve, generated by the turnover of the water column in December, was being continuously depleted until the May minimum temperature. The oxygen reserve was then replenished by the late June turnover and reached the second minimum in September; however, the oxygen consumption was slow; for instance, integrally only 40 and 50 g O_2 m^{-2} yr^{-1} was taken up by the water and sediments, respectively, compared with 140–560 g O_2 m^{-2} yr^{-1} consumed by sediments in western Lake Erie [32]. Seasonal amplitude was small, and simulated oxygen concentration in the deepest grid's depth of 90 m in Big Onego (site 4 in Fig. 9, *f*, *g* in [11]) alternated interannually between maximums of 11.98 ± 0.22 g O_2 m^{-3} and minimums of 7.00 ± 1.84 g O_2 m^{-3}. These averages far exceeded the oxygen deficit values that would trigger and maintain the "vicious circle" of eutrophication, which, in the Baltic Sea, is driven by the intensification of denitrification under hypoxic conditions and phosphate release from anoxic bottoms, thus, lowering the DIN: DIP ratio and leading to the expansion of diazotrophic cyanobacteria blooms [33, 34]. The "vicious circle" incidence seems unlikely in Lake Onego yet, because of DIN concentrations being high and deep layers being ventilated twice a year (cf. Fig. 2, *a*). For example, explanations for the ongoing eutrophication and emergent cyanobacteria blooms in large boreal lakes, such as Lake Winnipeg and Lake Superior, are sought in the immediate effects of changing external inputs and impacts rather than in the evolution of internal biogeochemical cycling [26, 35–38].

3. Spatial features of seasonal dynamics

These described general interactions are largely occurring in the vast deep-water areas. In coastal areas shallower than 30 m, which occupy approximately 53 % of Lake Onego's area, especially in the bays, dynamics differ (Fig. 2; see also Fig. 9, *d*, *e* in [11]), mainly because of the continuous sustenance of PP by nutrients regenerated at- and released from the bottom sediments situated within the epilimnion. Besides spatial gradients between coastal areas and deep-water areas (cf. Fig. 9 in [11]), the seasonal dynamics are clearly seen in large scale spatial features presented in Fig. 3 for the time of the winter maximum nutrient accumulation (cf. Table 1) and the mid-August cross-sections.

The reversed vertical distribution of the water temperature in winter (cf. Fig. 2, *a*) is replaced by stratification separating water body on epilimnion and hypolimnion (Fig. 3, *a*, see also Fig. 6 in [11]). With a shallowing of the lake towards the south, hypolimnion layers become less stratified due to intensified mixing performed by the variety of water movements [8]. Apparently, such movements are less effective during the ice period, that is before the spring turnover of the water column (Fig. 2, *a*). Such hydrodynamical "passiveness" results in near bottom accumulation of phosphorus both sinking down from the above layers and released due to mineralization in the water column and sediments (Fig. 3, *b*, *c*). Later, during vegetational season nutrients are, first, almost homogenized vertically by the spring turnover and then start accumulating in the hypolimnion again (Fig. 2, *b*, *c*). Such development and distribution can also be seen in very sparse and irregular measurements ([39, 40], see maps and cross-sections at p. 85 in [9]).

4. Biogeochemical fluxes and budgets

There is almost no historical or contemporary information about external and, especially, internal biogeochemical fluxes based on field measurements, except for instances of compiled nutrient inputs and PP estimates. Instead, we present two subsets of 5-year averages obtained by the annual integration of the simulated three-dimensional fields of concentrations and selected biogeochemical fluxes over the entire Lake Onego (Table 2, see Fig. 1 and 2 in [11]). We used these subsets, reconstructed by internally consistent numerical reanalysis, to demonstrate and highlight the most important features of the biogeochemical cycles of Lake Onego.

First, the comparison of external exchanges with internal cycling clearly showed that nutrient cycles were driven mostly by internal biogeochemical processes. Annual integrals of both the external inputs of nutrients into Lake Onego and their removal: a) by a permanent sediment burial, b) with the Svir River outflow, and c) by denitrification, were several times smaller than the stocks already accumulated and cycling in the water body and in the bottom sedi-

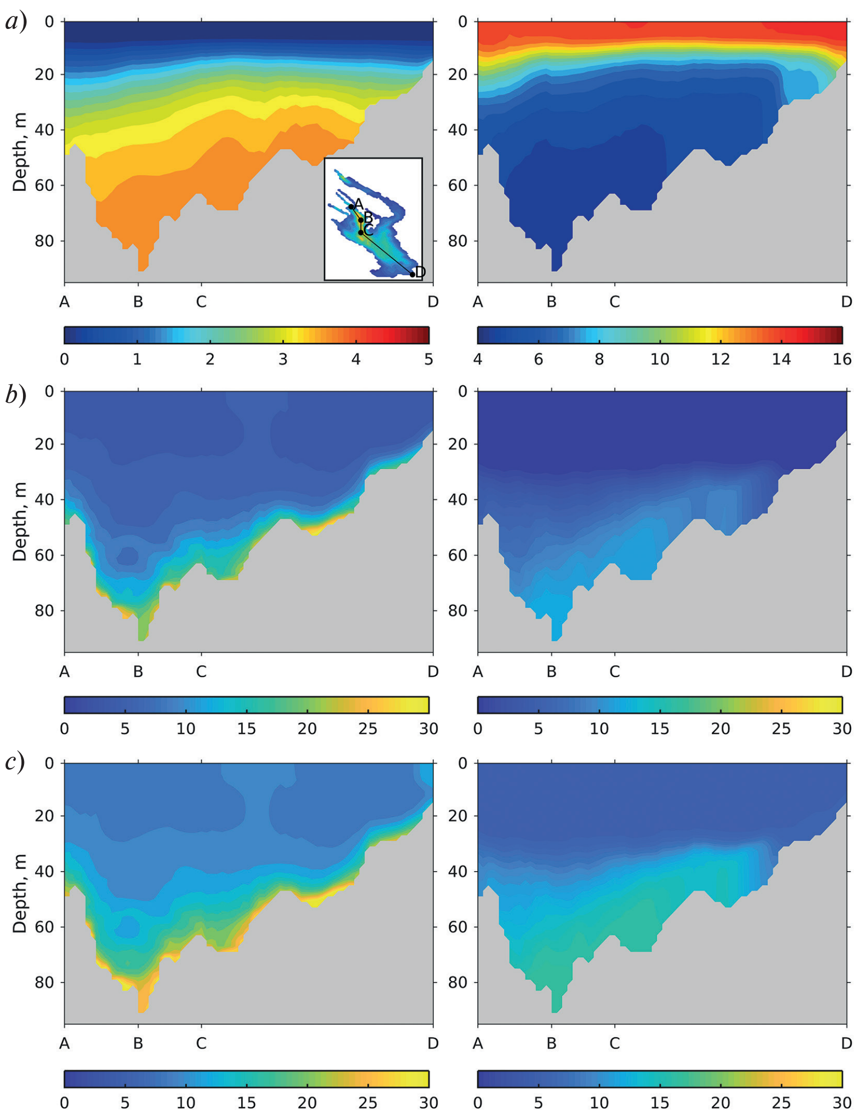

Fig. 3. Simulated long-term average (1985–2015) distribution of water temperature, °C (*a*, note different colour palette scales), DIP, mg P m^{-3}(*b*), and TP mg P m^{-3} (*c*) at cross-section ABCD on Day 118 (left panel) and Day 227 (right panel). Note different colour palette scales

ments. Only 17 % of P and 25 % of N were provided to autotrophs externally, while the rest was supported by inorganic nutrients regenerated in the water column and released from the sediments. The prevalence of internal cycling over external impacts is common in neighbouring Baltic Sea ecosystems [41–43] and in the remote Lake Superior [22].

The balance between external exchanges and internal cycling is usually expressed with a “nutrient residence time”, calculated as the ratio of integral nutrient stock to the amount causing the annual change of the stock, where total external input traditionally serves as a denominator. In addition, by estimating nutrient residence times from long-term reanalysis with seasonal and interannual variations (see Fig. 3 and 8 in [11]), we could also relate the total stock to a half-sum of sources and sinks. For instance, limnetic P residence time based on the 1985–2015 averages was calculated as the integral TP amount (2,681 t P) divided by the half-sum of total P input (834 t P yr^{-1}), export via the Svir River (131 t P yr^{-1}), sedimentation out of the water body (3,371 t P yr^{-1}), and phosphate release from the sediments back into the water body (2,401 t P yr^{-1}).

Limnetic nutrient residence times, calculated relatively to either only external inputs or accounting for the water-bottom exchange, were short (Table 2), explaining the fast responsiveness of Lake Onego’s waters to interannual variations of external effects (see Fig. 3 and 8 in [11]). The residence time for an external P input of 3.6 years has also been estimated on the basis of field observations [44]. Although with some controversy generated by the different

Table 2

Simulated annual biogeochemical fluxes and total amounts of nutrients, integrated over the entire Lake Onego and averaged for the start and end 5-year time intervals. Nutrient residence times are estimated for the entire 1985–2015 simulated time interval

Parameters	Phosphorus fluxes, t P yr^{-1}		Nitrogen fluxes, t N yr^{-1}	
	1985–1990	2011–2015	1985–1990	2011–2015
External exchange				
Total nutrient input	814	862	18.662	13.649
Dissolved inorganic	395	431	5.724	4.950
Labile dissolved organic	356	366	4.573	3.338
Export via Svir River	136	149	9.645	5.605
Permanent burial[*]	653	688	1.459	1.555
Denitrification			7.221	7.638
Internal cycling and bottom-water exchange				
Uptake by autotrophs	4.327	4.708	30.289	32.958
Total limnetic recycling	1.586	1.731	13.628	13.189
Sedimentation	3.278	3.542	23.048	24.920
Sediment release	2.334	2.483	13.669	14.897
Total amount[**], tonnes				
Water column	2.641	2.832	224.711	168.598
Sediments	39.743	41.757	88.798	94.190
System	42.383	44.588	313.509	262.788
Nutrient residence time (1985–2015), years				
Limnetic[***]	0.8 (3.2)		6.4 (12.4)	
Sediments	12.2		3.8	
System	46.9		17.4	

[*] — Simulated with uniform burial rate of 0.8 mm yr^{-1}, well fit to the observed range of 0.2–1.5 mm yr^{-1} [45].

[**] — Average calculated on January 1 of every simulated year.

[***] — Average total amount divided by the half-sum of sources and sinks (average total amount divided by average external input).

methods of calculation, similar P residence times, from a few months to several years, have been estimated for Lake Superior [22]. However, N residence time, despite being reevaluated in [22] to 55 years from an older estimate of 160 years, is still approximately ten times longer in Lake Superior than in Lake Onego. Such estimates, which are traditionally made only for water bodies and do neglect nutrient stocks and processes in the surface biogeochemically active layer of the bottom sediments, can be quite misleading. For the entire Lake Onego ecosystem, longer residence times of 47 and 17 years for P and N, respectively, were calculated when accounting for both the water and sediment stocks. Consequently, in contrast to short-term responses to external inputs, the long-term reaction of the entire phosphorus-limited Lake Onego ecosystem would be slow, as seen in Fig. 8 in [11].

The lower buffer capacity with respect to nitrogen was explained by denitrification, which is inevitably set at some depth in the pore waters over the entire sediment area but is sometimes overlooked in studies of large boreal lakes [22, 26, 46, 47]. Nowadays, denitrification in Lake Onego removes 56 % of the total nitrogen input or over 90 % of the bioavailable nitrogen input. The Lake Onego long-term lake-wide mean denitrification rate of 0.8 g N m^{-2} yr^{-1} belongs within the range 0.12–7 g N m^{-2} yr^{-1} that was compiled for oligotrophic and oligo-mesotrophic lakes in [48]. These authors also reported an average rate of 13 g N m^{-2} yr^{-1} when measured at multiple littoral sites in the oligotrophic Lake Memphremagog (located at approximately 45° N) with water temperatures exceeding 18 °C. Similarly, high rates (13 g N m^{-2} yr^{-1} in 2016 and 5 g N m^{-2} yr^{-1} in 2017) were measured in the eutrophic western basin of Lake Erie [32]. Measurements at 86 different stations across lakes Superior, Huron, Erie, and Ontario varied both spatially and temporally from 0.01 to about 400 g N m^{-2} yr^{-1}, covering wide ranges within each lake and exhibiting significant overlapping; for example, the denitrification rates measured in the Lake Superior bays were closer to the rates in Lake Erie and Huron than at other deep sites in Lake Superior [49]. Evidently, spatial inhomogeneity and seasonal variations also exist in Lake Onego (see Figs. 8, *f* and 9, *g* in [11]. For example, at the deepest site 4 (see Fig. 9, *g* in [11]) the denitrification rate reached up to 5 ± 0.3 g N m^{-2} yr^{-1} (mean ± SD) in July — August, i.e. after sedimentation of the freshly produced detritus.

Together with burial, denitrification removes approximately 40 % of organic nitrogen that reaches the bottom surface (cf. Table 2); the rest is returned to the water column at an average rate of 1.5 g N m^{-2} yr^{-1}, which is comparable to 0.9 g N m^{-2} yr^{-1} calculated here as a difference between nitrification and denitrification rates measured in the sediment core incubation in Lake Superior [50]. In Lake Onego, an almost equal share of inorganic nitrogen was provided by the total recycling of 1.4 g N m^{-2} yr^{-1} in the water body.

In Lake Onego, the bottom release of phosphorus (0.26 g P m^{-2} yr^{-1}), which returns approximately 70% of the annual sedimentation to the water column, is more important for internal cycling than limnetic phosphorus recycling (0.18 g P m^{-2} yr^{-1}). These values are within the same order of magnitude as mineralization rates of organic phosphorus (0.4–1.2 g P m^{-2} yr^{-1}) in the water column of Lake Superior [22] and bottom release rates of 0.6 g P m^{-2} yr^{-1} in western Lake Erie [32], or extrapolations of 0.4 g P m^{-2} yr^{-1} which were estimated over Lake Winnipeg by [51]. In the neighbouring oligotrophic Lake Ladoga, an extensive sediment survey resulted in a range of 0.02–0.24 g P m^{-2} d^{-1} [52].

5. Conclusions

1. The presented seasonal dynamics, including its spatial features as well as the analysis of simulated biogeochemical fluxes have further confirmed plausibility of our reanalysis and suitability of the model for studies of the past, present, and future Lake Onego ecosystem at necessary spatial and temporal scales.
2. This reanalysis generated regionally new phenological knowledge that was previously missed due to a lack of regular winter observations. The analysis of the simulation quantified that the spring phytoplankton bloom, which was previously overlooked, occurred at the beginning of May and contributed to approximately half of the annual primary production of the lake. This bloom was triggered by increasing sun radiation rather than an insignificant rise in water temperature.
3. Coherent nutrient budgets built on the simulated stocks and biogeochemical fluxes integrated over the water body and bottom sediments, which are often neglected in some other studies, revealed a high buffer capacity of Lake Onego, which is also reflected in long phosphorus and nitrogen residence times, 47 and 17 years, respectively. Effective buffering is defined by an internal biogeochemical cycling of nutrients within and between the pelagic and benthic subsystems, which is much more intensive than external inputs and exchange.
4. The shorter nitrogen residence time was explained by sediment denitrification, which is often ignored in studies of other large lakes, together with insufficient attention to the sediments and their role in biogeochemical cycling.

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