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Atmospheric stilling offsets the benefits from reduced nutrient loading in a large shallow lake

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Abstract

As part of a global phenomenon, a 30% decrease in average wind speed since 1996 in southern Estonia together with more frequent easterly winds resulted in 47% decrease in bottom shear stress in the large (270 km²), shallow (mean depth 2.8 m), and eutrophic Lake Võrtsjärv. Following a peak in eutrophication pressure in the 1970s–80s, the concentrations of total nutrients were declining. Nonmetric Multidimensional Scaling (NMDS) ordination of a 54-year phytoplankton community composition time-series (1964–2017) revealed three distinct periods with breaking points coinciding with changes in wind and/or water level. Contrary to expectations, we detected no decrease in optically active substances that could be related to wind stilling, whereas phytoplankton biomass showed an increasing trend despite reduced nutrient levels. Here we show how opening of the "light niche," caused by declining amount of suspended sediments, was capitalized and filled by the light-limited phytoplankton community. We suggest that wind stilling is another global factor, complementary to climate warming that counteracts eutrophication mitigation in lakes and may provide a challenge to assessment of the lake ecological status.

Recently a number of studies (e.g., McVicar and Roderick 2010; Vautard et al. 2010; Bichet et al. 2012) have shown that surface winds have slacked in several regions of the world. Decreasing over land wind speeds have been reported, for example, from central Mediterranean and Adriatic areas (Pirazzoli and Tomasin 2003), East Asia (Xu et al. 2006), west coast of Canada (Tuller 2004), Australia (Roderick et al. 2007), and northern Europe (Woolway et al. 2017). Based on data from 822 surface weather stations, Vautard et al. (2010) showed that between 1979 and 2008 surface wind speeds have declined by 5–15% (on average 0.11 m s^{-1} per decade) over almost all continental areas (at 73% of surface stations) in the northern mid-latitudes. The decreasing trend over the past 30 years was rather gradual; however in Europe the aforementioned authors found major drops in wind speed in years 1996 and 2000. Changes in wind speeds may differ by seasons, e.g., in Madison, WI, USA, Magee and Wu (2017) described

abrupt decreases in yearly, summer and fall wind speeds in 1994, spring wind speed in 1996, and winter wind speed in 1997. In a review of 148 studies reporting terrestrial wind speed trends, McVicar et al. (2012) concluded that terrestrial stilling was a widespread phenomenon across the globe. The suggested causes for the stilling (see recent review by Wu et al. 2018), such as changes in atmospheric circulation patterns (Lu et al. 2007; He and Soden 2015), gradients in sea surface temperature (Klink 1999; He and Soden 2015), aerosol emissions (Xu et al. 2006; Guo et al. 2011), and increasing surface roughness (Vautard et al. 2010), are likely to have different importance by region (Bichet et al. 2012). The widespread terrestrial stilling is, however, counterbalanced by a 50–60% increase in duration and severity of storms over North Atlantic and North Pacific since 1949 (Emanuel 2005).

As a global phenomenon, terrestrial atmospheric stilling has important implications for inland waters through disruption of the thermal stratification (Magee and Wu 2017; Woolway et al. 2017) and energy dissipation (Woolway and Simpson 2017; Woolway et al. 2018). In shallow lakes, wind stilling results in lower bottom shear stress that is a function of ground wind speed, wind fetch, and water depth (Wu et al. 2016) and represents the main force causing sediment erosion. Models have shown that the effect of wind on water temperature and stratification may be greater than that of increasing air temperature

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(Magee and Wu 2017; Woolway et al. 2017). Longer lasting stratification due to stilling winds can enhance iron-bound phosphorus release from bottom sediments of deeper lakes becoming anoxic (Bormans et al. 2016), but can decrease the frequency of aerobic phosphorus release pulses from shallow lake sediments caused by sediment resuspension (Holmroos et al. 2009; Kragh et al. 2017). As shown by Holmroos et al. (2009), resuspensionmediated internal loading is often the main mechanism bringing nutrients into the water column, especially in shallow lakes. A shift from pulsed nutrient supply to slower changes in nutrients ratios over seasonal scales can shift the balance between r- and Kstrategists among phytoplankton species and can lead to more complete use of resources due to coexisting complementary lifehistory traits (Papanikolopoulou et al. 2018). The r/K selection (MacArthur and Wilson 1967) opposes fast reproducing and growing "opportunistic" species that exploit less-crowded, sometimes temporary, ecological niches (r-strategists) with strong tolerant competitors in crowded niches living at densities close to carrying capacity of the environment (K-strategists). Stronger stratification in shallow polymictic lakes selects for motile species like cyanobacteria and flagellates (Wilhelm and Adrian 2008) as they can move vertically in the water column. Studies of Lake Taihu (China) have shown that weaker winds caused a vertical gradient in Microcystis biomass with high surface chlorophyll-a concentrations and increased bloom area (Wu et al. 2015). Wang et al. (2016) distinguished three components of wind influence on harmful algal surface blooms: a disturbance impact on cyanobacterial proliferation, a nutrient impact by sediment release, and a transportation impact by wind and wave induced surface drift. Two other important impacts of wind-induced sediment resuspension are its influence on phytoplankton community composition through entrainment of meroplanktonic algae from the lakebed to the water column, and on primary production through increased light attenuation (Schallenberg and Burns 2004). Thus, irrespective of the mechanism, sediment disturbance results in a loss of water transparency. Hence, we expect that wind stilling will cause the opposite-a decrease in light attenuation and improvement of water transparency.

Recently, the effect of wind stilling on the thermal stratification of a large shallow polymictic lake (Võrtsjärv) in Estonia was investigated, finding that the abrupt decrease in surface wind speed since mid-1990s resulted in a higher number of stratified days (Woolway et al. 2017). We expected that this change leading to less frequent sediment disturbance in this shallow lake would result in better water transparency as suspended sediments are one of the reasons of high turbidity in the lake. In contrast to Lake Taihu where the scum forming species benefitted from calm periods (Wu et al. 2015), Võrtsjärv is dominated by thin filamentous Limnothrix species evenly distributed in the water column due to their nearly neutral buoyancy and slow speed of floating or sinking (Walsby 2005). We expected that less sediment disturbance would result in less nutrient release from the sediment that would rather decrease than increase phytoplankton biomass and in turn contribute to transparency improvement. However, when checking this in the long-term record of water quality data available for this lake, a contradiction became apparent: There was no improvement in water transparency or decrease in phytoplankton abundance since mid-1990s as could be expected from the considerable wind stilling and decreasing trends in nutrient concentrations. Here we provide a mechanistic explanation to this contradiction by analyzing the long-term time series of phytoplankton, nutrients, and optically active substances to uncover relationship with drivers of wind stilling in Lake Võrtsjärv. Previous studies have shown the dominating role of water-level changes in controlling the water quality parameters in Võrtsjärv. Stronger sediment resuspension at low WLs enriches the water with suspended solids resulting in lower water transparency but improved average light conditions in the water column by "cutting off" less illuminated and less productive deeper layers (Nõges and Järvet 1995; Nõges and Nõges 1999). Enhanced sediment phosphorus release and denitrification at low WLs cause a decline in the N:P ratio and a shift in all common trophic state indicators (total phosphorus concentration, chlorophyll-a, phytoplankton biomass, Secchi depth) toward a higher trophic state (Nõges and Nõges 1998; Tuvikene et al. 2011). Given the strong influence of water-level changes on Võrtsjärv ecosystem, this parameter was added as a cofactor in our analysis.

Thus, this study investigates the following hypotheses:

- 1. Lower wind speeds cause lower bottom shear stress resulting in less frequent episodes of aerobic phosphorus (P) release and through it suppresses small, fast-growing phytoplankton species (*r*-strategists).
- 2. Lower bottom shear stress results in less frequent occurrence of meroplanktonic (benthic, periphytic) species in phytoplankton as there is less chance for them to be resuspended.
- 3. Longer thermal stratification episodes favor motile (flagellate) species able to migrate to optimize their light and nutrient supply, and scum-forming cyanobacteria requiring calm conditions for bloom formation.
- 4. Less frequent sediment disturbance stimulates the growth of light-limited slow growing phytoplankton dominants (*K*-strategists) and their biomass will increase as suggested by an increasing contribution of chlorophyll-*a* and decreasing contribution of suspended solids to total light attenuation. The plausible mechanism for this is based on compensatory growth of the light limited species on the account of additional light resource caused by decreasing light attenuation by suspended sediments.

Methods

Site description

Lake Võrtsjärv is a large (area 270 km²), shallow (mean depth 2.8 m, maximum 6 m), eutrophic lake located in the central part of Estonia (58°16′N, 26°02′E; Fig. 1). Following peak loadings of nutrients in the 1980s reaching 16.4 g m⁻² y⁻¹ of total nitrogen (TN) and 0.7 g m⁻² y⁻¹ of total phosphorus (TP), the loadings steadily declined to approximately 5.4 g TN m⁻² y⁻¹ and 0.1 g TP

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Fig. 1. Location of Lake Võrtsjärv and the sampling stations.

 $m^{-2}~y^{-1}$ by the 2000s. During 1994–2009, the lake was characterized by the following average concentrations: TN 1.4 \pm 0.6 mg l $^{-1}$, TP 50 \pm 25 μ g l $^{-1}$, and chlorophyll-a 31 \pm 23 μ g l $^{-1}$ (Nõges and Nõges 2012). Throughout the ice-free period, the Secchi depth does not exceed 1 m.

Due to the shallowness, the lake is lacking a real accumulation area sensu Håkanson (1977), and even the deeper parts are subjected to periodic resuspension during storms. A north– south transition from sandy silt, silt, silty clay to gyttja (organic rich mud) characterize the bottom sediments, while two thirds of the bottom are covered with gyttja (Raukas 2004). The water level (WL) of the lake is unregulated, with a 1.4 m mean annual amplitude of WL change and a maximum range of 3.2 m. The latter corresponds to a 1.4-fold difference in the lake area, a 2.4-fold difference in the mean depth and a three-fold difference in lake volume (Nõges and Nõges 1999).

The lake phytoplankton is represented by a *Limnothrix*-type assemblage near-continuously dominated (60–90% of the total biomass as seasonal average) by the slenderer species of

Oscillatoriales-Planktolyngbya limnetica (Lemm.) J. Komárková-Legnerová. Limnothrix redekei (Goor) Meffert. and L. planktonica (Wołosz.) Meffert. These species have among the highest adaptive capacities of any algae to low average insolation (Reynolds 1994). Since late 1970s when the two Limnothrix species outcompeted P. limnetica, which still occurs in moderate numbers, no major change in the phytoplankton community composition occurred, while the total biomass has slowly increased over the years. The Limnothrix species representing slow growing K-strategists are sensitive to hydraulic flushing and cannot colonize areas with short water retention time (Idrizaj et al. 2016). Although enhanced gas-vacuolation reaching up to 50% of cell volume has been described in some strains of L. redekei in winter (Gkelis et al. 2005), the gas-vacuolation in Võrtsjärv remains low and no gradients in the vertical distribution of the Limnothrix species have been observed. Among diatoms forming the second abundant group in Võrtsjärv, the bulk of the biomass is built up by large filamentous Aulacoseira spp. accompanied mostly by benthic and periphytic species from genera Surirella, Gyrosigma, Navicula, and Nitschia during windy periods.

Meteorological variables

Daily wind speed (at 10 m height) and direction data were obtained from the nearest to the lake meteorological station (Tõravere, 20 km), daily WL, and surface water temperatures (SWT) for 1964–2017 through the Estonian Environment Agency. There have been three different instruments used for wind measurements in the Tõravere station (Jaagus and Kull 2011). Until 1976, wind speed and direction were visually observed eight times per day using Wild's wind vanes. Since November 1976, automatic anemo-rhumbometers, and since September 2003 automatic weather stations have been used. As no jumps occur in wind data at these times, it can be assumed that the change of instruments had no major effect on wind records.

Lake sampling

Sampling for water chemistry and phytoplankton, including water transparency measurements with a Secchi disk was carried out monthly, in some years fortnightly or weekly from 1 to 4 pelagic stations, whereas the length of the time series differed for different parameters. We had the longest time series for phytoplankton composition and biomass (1964-2017) followed by Secchi depth (SD) (1966–2017). We used data on chlorophyll-a (Chl-a), phaeopigments (Phaeo), colored dissolved organic matter (CDOM), and total suspended solids (TSS) measured since 1989, and those of TN and TP since 1994. Water was taken with a Ruttner sampler from 0.5 m depth or vertically with 1-m step and mixed in a bigger vessel from which an integrated sample was taken. As the lake is mostly fully mixed and no significant differences caused by sampling method were found between surface and integrated values of the main algal group (cyanobacteria and diatoms) biomasses, total biomass, and number of species (n of parallel measurements 92, p of Student's t-test between 0.39 and

0.88 for different variables), the surface and integrated samples were pooled for the analysis. Similarly the samples from the four pelagic stations were pooled for correlation analyses as our previous study (Nõges and Tuvikene 2012) found no significant differences between them.

Analytical methods and calculations Bottom shear stress

We approximated wind directions to the four cardinal and four intercardinal directions and calculated the corresponding wind fetch as the average cross section of the lake surface in these directions. Using wind speed, wind fetch, and WL of the water sampling day and of 2 days before it as input variables, we calculated the 3-day average bottom shear stress (Shear3D) using the semi-empirical Sverdrup-Munck-Bretschneider (SMB) equations described in detail by Wu et al. (2016). The wave height and period are calculated using fetch, storm duration, and wind speed. Further, the elliptical orbital motion on the bottom is calculated from the linear wave theory. On the basis of the maximum velocity on the bottom and the friction factor caused by waves, the shear stress caused by waves is calculated. We calculated the shear stress for the water depth equal to the mean depth of the lake depending of WL. Within the range of registered changes in WL (in meters above sea level), the mean depth of the lake (m) can be calculated according to Nõges and Järvet (1995):

$$z_{av} = 0.741 * WL - 22.26 (R^2 = 0.90; p < 0.01)$$
 (1)

To calculate the frequency of sediment resuspension events, we applied two critical shear stress levels, 0.04 N m^{-2} and 0.05 N m^{-2} , delimiting the range described for sand, silt, fine silt, and mud sediments in large shallow lakes Erie (Sheng and Lick 1979), Balaton (Luettich Jr et al. 1990), and Okeechobee (Sheng et al. 1991).

Optical variables

Secchi depth (SD) was the only optical variable measured in each sampling occasion. We converted SD into diffuse attenuation coefficient (k_d) using the empirical relationship found for Võrtsjärv by Reinart and Nõges (2004) (see Supporting Information Fig. S1):

$$k_{\rm d} = 1.95 \,{\rm SD}^{-0.74} \,({\rm R}^2 = 0.89; p < 0.001)$$
 (2)

Based on these k_d values, we calculated the euphotic zone as the layer within which photosynthetically active radiation is attenuated to 1% of its surface value (Kirk 1994):

$$z_{\rm eu} = \ln 100 / k_{\rm d} = 4.605 / k_{\rm d} \tag{3}$$

The light field experienced by phytoplankton in the mixed water column depends besides the optical properties of water also on the mixing depth. Considering Võrtsjärv as a fully mixed water body (Laas et al. 2012), we used the mean depth of the lake (Eq. 1) as the mixing depth ($z_{mix} = z_{av}$) and calculated the mixing to euphotic depth ratio to characterize the underwater light conditions as z_{mix} / z_{eu} .

To assess the changes in the relative role of different optically active substances (OAS) in total light attenuation, we applied the principle that the total attenuation is the sum of attenuations caused by pure water (k_W) and the different OAS (Åberg and Rodhe 1942) each of which is a product of its concentration and specific attenuation coefficient (C'). Considering the latter as a constant, the attenuation caused by different OAS is proportional to their concentration. As Estonia belongs to the hemiboreal climatic region, the main OAS in lakes are phytoplankton pigments, TSS, and CDOM.

$$k_{\rm d} = k_{\rm W} + k_{\rm Chl} + k_{\rm TSS} + k_{\rm CDOM} = k_{\rm dW} + C'_{\rm Chl} \, \text{Chl} - a + C'_{\rm TSS} \, \text{TSS}$$

+ $C'_{\rm CDOM} \, \text{CDOM}$ (4)

The attenuation caused by water itself can be omitted because of its marginal importance (approximately 1% in Võrtsjärv; Nõges 2000) compared to other OAS. We used Chl-a as the best available rough proxy for all phytoplankton pigments whereas the light absorption by accessory pigments was not explicitly considered. We used the specific attenuation coefficient of $0.02 \text{ m}^2 \text{ mg}^{-1}$ for chlorophyll (C'_{Chl}) measured as the blue absorption maximum at 440 nm in Võrtsjärv in July 2008 (Paavel et al. 2016). We used the A400F value as the measure for CDOM concentration. According to our earlier study (Nõges 2000), the light attenuation by Chl-a and CDOM were of similar magnitude. The concentration of TSS (in mg L^{-1}) was measured in the lab by weighing method (see next paragraph). TSS is a heterogeneous component that contains varying proportion of phytoplankton, organic and mineral particles suspended in the water column, all having different specific weight and optical properties. Because of its heterogeneous composition, TSS concentration is a poor proxy for its optical effect. Therefore, the particle induced attenuation (k_{TSS}) was back-calculated from the optically measured variables (k_d , k_{Chl} , and k_{CDOM}) using the Solver function in Microsoft Excel. The nonlinear Solver algorithm reconstructed k_{TSS} by minimizing the difference between k_{Chl} and k_{CDOM} , while simultaneously constraining both to positive values. As we were interested in the dynamics of OAS rather than the absolute attenuation values caused by them, we considered this approach robust for the purpose.

Chemical analyses

Chemical analyses were done at Tartu Environmental Research Centre Ltd. TN and TP were measured in nonfiltered water samples spectrophotometrically after oxidative and hydrolytic digestion in a UV- and a thermo-reactor following the standards ISO 29441 for TN and ISO 15681-2 for TP. TSS were measured by filtration of water through preweighed glass fiber filters. The filter was then dried at 105°C and the mass of the residue retained on the filter was determined by weighing (standard EVS-EN 872). CDOM was measured in 5-cm cuvettes as spectrophotometric absorbance in filtered (Whatman GF-F filter) water at 400 nm (A_{400F} ; Kallio et al. 2005).

Phytoplankton and pigment analyses

Before 1994, phytoplankton samples were fixed with 2% neutralized formalin and counted in hemocytometer cells using a light microscope. Since 1994, the samples were fixed by Lugol's iodine and counted under inverted microscope using the Utermöhl (1958) method (for method details, see Nõges et al. 2010). Species were identified to the lowest possible taxonomic level and counted until reaching at least 400 counting units per sample. Relationships with environmental parameters were analyzed at order, species, and functional trait level. We included three orders of cyanobacteria (Oscillatoriales, Nostocales, Chroococcales), two orders of chlorophytes (Chlorococcales and Desmidiales), joined crypto-, chryso-, dino-, and euglenophytes into flagellates and split diatoms into planktonic and benthic/periphytic species for our analyses taking the habitat preferences from Timm (1973).

For pigments we followed the procedure recommended by Edler (1979). Approximately 100 mL of water was filtered through 47 mm Whatman GF-F filters. The moist filter was placed in a centrifuge tube (with a cap) prefilled with 5 mL of 100% acetone and put for 24 h in a fridge at 4°C for pigment extraction. Following extraction, samples were shook and then centrifuged for 5 min to remove filter and cell debris. Readings of spectrophotometric absorption were taken at 630 and 647 nm and at the peak value in the range 662-665 nm (Chl-a absorption maximum). Reading at 750 nm was used to correct for light scattering. Chl-a concentration was calculated according to Jeffrey and Humphrey (1975). For measuring Phaeo, the extract was then acidified with two drops of 1.2 M HCl and readings were repeated in the range of 662-665 nm (maximum) and at 750 nm. Phaeo concentrations were calculated according to Lorenzen (1967) equations. The ratio of Phaeo to Chl-a, a marker of phytoplankton degradation (Walker et al. 2008), was used as a proxy of sediment resuspension.



Fig. 2. Changes in daily average wind speed measured at Tõravere meteorological station from 1964 to 2016.

Statistical methods

To detect long-term changes in phytoplankton composition, we used Nonmetric Multidimensional Scaling (NMDS). NMDS is commonly considered as the most robust unconstrained ordination method in community ecology (Legendre and Legendre 1998). It aims at collapsing information from multiple dimensions (e.g., from multiple communities, sites, etc.) into just a few. Using rank orders instead of distances makes the NMDS technique able to accommodate a diversity of different types of data (Ramette 2007). First, we constructed community matrices from quantitative biomass values with species in columns and samples in rows. To stabilize variability, the community matrices were square root transformed, followed by Wisconsin double standardization (first, species divided by their maxima; second, samples divided by sample totals). From the community matrix, a Bray-Curtis dissimilarity matrix was calculated and subjected to NMDS (metaMDS with two axis; "Vegan" library in R). We

Table 1. Wind forcing related parameters (\pm standard deviation) for ice-free periods in Lake Võrtsjärv before and after the onset of atmospheric stilling in 1996. *n* – number of observations, *p* – statistical probability of the absence of difference between the mean values and variances.

	Years 1966–1995	Years 1996-2016	%	р	р
Wind forcing related parameter	<i>n</i> = 7048	<i>n</i> = 5118	change	means	variances
Average daily wind speed, m s ⁻¹	3.7 ± 1.7	2.6 ± 1.1	-30	0.0000	0.0000
Average daily wind fetch, km	13.2 ± 3.2	12.2 ± 2.6	-8	0.0000	0.0000
Average water depth, m	$\textbf{2.63} \pm \textbf{0.43}$	$\textbf{2.56} \pm \textbf{0.42}$	-3	0.0000	0.3944
Average daily shear stress, N m ⁻²	$\textbf{0.14} \pm \textbf{0.09}$	$\textbf{0.08} \pm \textbf{0.06}$	-43	0.0000	0.0000
% of ice-free days with critical shear stress exceeding 0.05 N m ⁻² and 0.04 N m ⁻²	86–95%	68–87%	-14	0.0000	1.0000

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Fig. 3. NMDS ordination plot of the 471 phytoplankton samples collected from Võrtsjärv Station 1 during ice-free periods over 54 years with fitted (**a**) aggregated phytoplankton variables and (**b**) environmental variables (see the goodness of fit in Supporting Information Table S1). The three periods were distinguished by the WBS analysis that is explained further.

fitted aggregated phytoplankton parameters and environmental variables on NMDS ordination of phytoplankton community composition using "envfit" function provided by "Vegan" package in R.

We used wild binary segmentation (WBS) technique to find change-points (jumps) in the mean values and variance of phytoplankton and hydro-meteorological data. Previous studies have indicated the superiority of WBS to other change-point detection methods (Baranowski and Fryzlewicz 2014; Sharma et al. 2016). To implement WBS methodology, we used the R packages "breakfast" and WBS (Baranowski and Fryzlewicz 2014; Fryzlewicz 2014). As the WBS approach requires homogeneous, equally distributed data, we applied it on regular monthly (May–October) data from Station 1, from which we had the most complete data set (471 ice free period phytoplankton samples collected over 53 years). In case of several samples from the same month, the data were not averaged to avoid inflation of species richness. Instead, the sample closest to the middle of the month was included in the analysis.

Results

Changes in wind forcing

Since the onset of atmospheric stilling in 1996, the average wind speed decreased from 3.7 to 2.6 m s⁻¹, i.e., by 30% compared to the preceding period 1966–1995 (Table 1, Fig. 2). Although the transition period lasted for 5 to 6 years before the mean wind speed stabilized at the lower plateau, the change was abrupt in the long term. There was a significant (p < 0.0001) decrease in both the mean and standard deviation of all wind-related parameters since 1996. As the wind change involved also more frequent westerly winds (not shown), the wind fetch shortened by 1 km due to the latitudinal shape of the lake. These two factors together resulted in 43% lower bottom shear stress in the period since 1996 compared to the



Fig. 4. Breaks detected in time series with WBS method: NMDS score 1 (a) and 2 (b), absolute water level according to the Baltic height system (c), and bottom shear stress showing the effect of atmospheric stilling (d).

earlier period of 1966–1995 that could not be compensated by the slightly (7 cm) lower mean depth of the lake in the later period (Table 1).

Hydro-meteorological forcing of phytoplankton community change

NMDS ordination of phytoplankton community composition revealed three clusters in the data (Fig. 3). The biomass of small coccal or colonial forms of green algae and cyanobacteria scaled negatively with NMDS1 (Fig. 3a) while the biomass of the dominants (filamentous cyanobacteria and diatoms) scaled positively with it showing that NMDS1 represented the division of phytoplankton taxa by size and growth rate, i.e., the r/K selection (see MacArthur and Wilson 1967). Among environmental variables, NMDS1 was negatively correlated with bottom shear stress and positively with the light limitation indicator z_{mix}/z_{eu} (Fig. 3b) showing that the smallsized *r*-strategists were supported by stronger sediment disturbance and suppressed by low light conditions. The highly shade tolerant slowly growing filamentous cyanobacteria, on the other end of the NMDS1 build up the bulk of phytoplankton biomass in Võrtsjärv and do not require turbulent mixing for staying in suspension. Along the r/K selection axis, this group is characterized as *K*-strategists.

The NMDS axis 2 scores scaled with the motility trait of taxa with flagellates and gas vacuolated cyanobacteria on one



Fig. 5. Long-term trends in the NMDS score 1 (a), and 2 (b), biomass of Oscillatoriales (c) and flagellated algae (d), total phytoplankton biomass (e), and the number of taxa in quantitative samples (f) from Võrtsjärv.

end and benthic diatoms on the other end of this distribution (Fig. 3a). Psychrophilic benthic and periphytic diatoms occur in plankton occasionally during strong mixing events in spring when the WLs are high after the flood peak, while greater biomass of cyanobacteria and flagellates is associated with warmer and more turbid (higher k_d) waters in summer when the WLs are generally low (Fig. 3b). The ability of flagellates to migrate makes them tolerant to high light attenuation; however, at high WLs they lose their mobility-related advantage. Strong polarity in NMDS2 caused by WL and SWT shows that this axis was partly characterizing the seasonality in this lake.

When plotted against time, WBS unveiled two jumps in both NMDS axes scores. The first jump between 1977–1978 in NMDS1 and 1978–1979 in NMDS2 coincided with an abrupt increase in the mean WL between 1977 and 1979 (Figs. 4a–c). The second jump in NMDS2 between 1996 and 1997 was concurrent with



Fig. 6. Percent distribution of phytoplankton biomass by classes over the three NMDS periods distinguished in phytoplankton community structure **(a)**, changes in average total phytoplankton biomass and the biggest "losers" and "winners" **(b)**. Height of the triangles shows significant biomass differences between the periods compared.

Table 2. Correlations of phytoplankton and environmental parameters with average bottom shear stress during 3 d including sampling day (Shear3D) and water level in the sampling day (WL). All variable were included as May–October average values for 53 years. Significance levels (*p*) given by asterisks: * <0.05, ** <0.01, *** <0.005, **** <0.001.

Variable	Shear3D	WL	
Flagellates	-0.65****	-0.06	
Oscillatoriales	-0.48****	0.03	
Total biomass	-0.39***	-0.20	
Nostocales	-0.37**	-0.32*	
Planktonic diatoms	-0.11	-0.25	
N of taxa	-0.09	-0.37**	
Desmidiales	-0.08	-0.06	
Chlorococcales	-0.05	-0.52****	
Benthic diatoms	-0.04	0.03	
Chroococcales	-0.01	-0.25	
SWT	-0.48****	-0.13	
k _d	-0.26	-0.66****	
z _{mix} /z _{eu}	-0.22	0.21	

the atmospheric stilling (Fig. 5(d)). Mainly the two jumps in NMDS2 split the 53-year time-series into three periods with distinct phytoplankton community structure forming the three clouds in the ordination graph (Fig. 3) and hereafter referred to as Period 1 (1964–1977), Period 2 (1978–1996), and Period 3 (1997–2017).

There has been a steady increase in total phytoplankton biomass over time, mostly related to an increase in slow-growing filamentous cyanobacteria (Oscillatoriales) and reflected in the common increasing trend with NMDS1 (Fig. 5a,c,e). The sudden drop in species richness and flagellate biomass in the end of the



Fig. 7. Long-term annual trend of total phosphorus (**a**) and total nitrogen (**b**) in Lake Võrtsjärv Station 1 over the period 1989–2017.



Fig. 8. Long-term changes in diffuse attenuation coefficient (**a**) and the mixing to euphotic depth ratio (**b**) in Võrtsjärv. Arrows indicate the onset of stilling.

1970s followed by a slow recovery were most strongly shaping the NMDS2 dynamics (Fig. 5b,d,f).

The relative share of the major phytoplankton classes in the total biomass remained rather stable over years with a slight increasing trend in cyanobacteria dominance, especially between Periods 2 and 3 (Fig. 6a). The biggest "losers" and "winners" were revealed by comparing the average biomasses changes at species level between Periods 1, 2, and 3. The species showing significant increase or decrease (Student's *t*-test, p < 0.05) were ordered by the effect size of the biomass difference. Figure 6b shows the differences for the three most abundant Oscillatoriales species whereas the other species showing significant differences were summed up to other significant "winners" and "losers" between the periods. The shift from Period 1 to Period 2 (reflected also in the jump in both NMDS scores) marked the change from *Planktolyngbya limnetica* domination in Period 1 to codomination of *Limnothrix planktonica* and *L. redekei* in Period 2. The change between Periods 2 and 3 expressed only in NMDS2 was characterized by a further decline of *P. limnetica*, decreasing share of *L. redekei* among the dominants and a boost of *L. planktonica* biomass (Fig. 6b).

Shear stress and WL

The jump in wind induced bottom shear stress series in 1996/97 coincided with the lowest WLs ever registered in Võrtsjärv and with the second jump in NMDS2 (Fig. 4). Correlation analysis showed that atmospheric stilling supported flagellates but Shear3D was significantly negatively related also with filamentous cyanobacteria, from both Oscillatoriales and Nostocales that build up the bulk of the total biomass in Võrtsjärv (Table 2). As stronger winds disable thermal stratification and equalize the temperature in the water column, Shear3D was negatively related with SWT. The first jump in both NMDS scores coincided with that in WL (Fig. 4). Low WL supported Chroococcales and Nostocales and increased taxa numbers (Table 2).

Nutrients

Over the period since 1989 covered by homogeneous data from the State Monitoring Program, the annual mean values of TN ranged from 1.1 to 3.2 mg L⁻¹ and those of TP from 0.035 to 0.072 mg L⁻¹. Statistically significant (p < 0.001) decreasing

Table 3. Pearson correlations between average wind forcing for 3 d before sampling, water level and optical variables: diffuse attenuation coefficient (k_d), concentrations of total suspended solids (TSS) and chlorophyll-*a* (Chl-*a*), light absorption in filtered water (A_{400F}) shown as CDOM, and the mixing depth to euphotic depth ratio (z_{mix}/z_{eu}) in three WBS periods. Significance levels (*p*) given by asterisks: * <0.05, ** <0.01, *** <0.005, *** <0.001.

	Period	k _d	TSS	Chl-a	СДОМ	z _{mix} /z _{eu}
Wind speed	1	0.33****	_	_	_	_
	2	0.14	0.23*	0.39****	-0.42****	-0.02
	3	-0.08	0.15	0.15	-0.04	0.05
Shear stress	1	0.31****	_	_	_	_
	2	0.12	0.19	0.21	-0.05	-0.08
	3	-0.03	0.13	0.28****	-0.16	0.02
Water level	1	-0.54****	_	_	_	_
	2	-0.54****	-0.36***	-0.51****	0.62****	0.49****
	3	-0.44****	-0.24***	-0.42****	0.74****	0.28****





Fig. 9. Modeled relative role of CDOM, TSS, and Chl-*a* in the total light attenuation coefficient k_d , and the proportion of phaeopigments in total pigments measured as Chl-*a*. The arrow indicates the onset of stilling.

trends occurred in both total nutrients (Fig. 7) being strongest for winter TN and autumn TP (not shown).

Changes in underwater light climate and OAS

The strongest light attenuation occurred in Võrtsjärv in Period 1 (Fig. 8a) but as it coincided with low WL (Fig. 4c), the light conditions in the water column remained generally better (lower $z_{\text{mix}}/z_{\text{eu}}$) than in later periods (Fig. 8b). In the period of atmospheric stilling, k_{d} increased again (from average 2.1 m⁻¹ to 2.4 m⁻¹, p < 0.001) after being low in Period 2. The ratio $z_{\text{mix}}/z_{\text{eu}}$ increased significantly from Period 1 to Period 2 (from average 2.4 to 3.5, p < 0.001) and remained at the same mean value but was more variable (SD from 0.97 to 1.24, p < 0.001) in Period 3.

WL had a major effect on all OAS increasing the concentrations of TSS and Chl-*a* at low WLs and those of CDOM at high WLs (Table 3). Lower TSS and Chl-*a* at high WL had a stronger effect on the optical properties (k_d) of water than the accompanying increase in CDOM resulting in better transparency (lower k_d) at higher WL. All correlations of WL with OAS and optical indicators were stronger in the windy Period 2, except the correlation with CDOM that became stronger in the calm Period 3. As a paradox, the worst light conditions (highest z_{mix}/z_{eu} values) occurred in the water column at high WL (r = 0.35, p < 0.001) when the k_d was lower (r = -0.47, p < 0.001). With increasing WL more CDOM enters the lake from the catchment through river inputs. The strong positive correlation between WL and CDOM implies that CDOM amplified the attenuating effect of increasing WLs.

Modeling of the relative role of the different OAS in the total light attenuation k_d (Fig. 9) showed a highly significant (p < 0.0001) increase in Chl-*a* contribution (k_{Chl} , from 25% to 36%) and a corresponding decrease in TSS contribution (k_{TSS} , from 60% to 50%) in the period of atmospheric stilling (see the scatter plots relating k_d with Chl-*a* and TSS in Supporting Information Fig. S2). No trend occurred in the CDOM contribution (k_{CDOM}) to the total light attenuation.

The proportion of Phaeo in total pigments measured as Chl-a was used as a marker of resuspended sediments, showing high variability in the windy period but stabilized at levels mostly below 0.2 in the calm Period 3 (Fig. 9).

Discussion

Our study showed two jumps occurring in the long-term phytoplankton community composition that split the 54-year time-series into three periods with discernible community structure. The first jump between 1977 and 1979 was related to a strong increase in WL causing deeper mixing. The strong positive correlation between WL and CDOM over the period of CDOM measurements (since 1989) suggests that the higher water in earlier years likely also contained more CDOM further deteriorating the light conditions. Decreased light levels in the mixed layer caused a replacement of dominant phytoplankton species with more shade tolerant ones. As this change was already discussed in Nõges et al. (2010), we will not repeat it here.

We hypothesized that lower wind speeds cause lower bottom shear stress resulting in less frequent episodes of aerobic P release and through it here, the suppressing of small, fast-growing phytoplankton species (r-strategists). Indeed, the NMDS score 1 showed a strong gradient along the r/K-selection axis and was negatively related to shear stress. The r-selected species of small body size and high growth rates, represented in Võrtsjärv by Chlorococcales, Chroococcales, and Desmidiales, were successful in periods of unstable environments during stronger wind and low WL. Being able to utilize short pulses of nutrients (Papanikolopoulou et al. 2018) released from aerobic sediments during resuspension episodes, numerous species from these groups developed in years of low WL in early 1970s and 2000s contributing to total species diversity. The K-strategists on the other end of the NMDS1 got an advantage during high water periods characterized by more stable conditions and lower average light levels in the deeper mixed water column. The typical representatives of this group were species of cyanobacteria belonging to Oscillatoriales and Nostocales but also the benthic diatoms, all being shade tolerant.

The z_{mix}/z_{eu} ratio showed a deterioration of light conditions in the lake since Period 2, together with increasing trends in Chl*a* and phytoplankton biomass, mostly accounted for by an increase in *Limnothrix* spp. belonging to Oscillatoriales. Cyanobacteria respond to light limitation with an increase in the light harvesting pigments, including accessory pigments phycocyanin and phycoerythrin, or change in the number of photosynthetic units (Rücker et al. 1995). Experiments with one of the dominant Oscillatoriales species, *Limnothrix redekei*, showed that under light-limited conditions, the growth rate increased linearly with daily light dose (Gibson 1987). Similarly, field studies in lakes where the mixed zone was deeper than the euphotic zone showed that growth of *L. redekei* was controlled mainly by light intensity (Meffert 1989). The competition between the two



Fig. 10. Conceptual diagram relating wind and phytoplankton biomass in a shallow eutrophic lake. Weakening winds reduce turbulent mixing resulting in less suspended sediments (1) and entrained meroplankton in the water column (2). Both processes reduce light attenuation by total suspended solids (TSS) and pigments envelope leaving more light for photosynthesis (3). Less aerobic P release from sediment reduces P availability for phytoplankton growth (4) that in light-limited conditions may not have a major effect. Besides suspended solids that attenuate light by absorption and scattering, total light attenuation (3) includes also light absorption by other optically active substances (OAS)—colored dissolved organic matter (CDOM) and pigments contained in both phytoplankton and sediments. In light-limited conditions, weakening light attenuation creates a "light niche" for photosynthesis enhancing phytoplankton growth. Increasing phytoplankton biomass fills this niche in the TSS and pigment envelope until self-attenuation reaches limiting levels for photosynthesis. This negative feedback loop controls the balance (triangle) between suspended sediments and phytoplankton biomass in the TSS and pigment envelope. Changes in water levels have a dual effect on light attenuation: Increasing water levels reduce the TSS and pigment envelope by weakening turbulent mixing (5) but deeper mixed layer amplifies the effect of all OAS. More CDOM leaching from the catchment increase water color during water-rich periods that effect on light attenuation is further amplified by higher water levels (6). Increased nutrient loading during water rich periods may shift the system toward stronger light limitation.

Limnothrix species in Võrtsjärv showed *L. planktonica* as a "winner" in the last period, while the biomass of *L. redekei* declined. This could be due to the positive effect of increased water temperature (Nõges and Nõges 2014) on *L. planktonica* that reaches its biomass peak later in the season than *L. redekei*, and has likely a higher temperature optimum. However, the success of *L. planktonica* may also be based on its allelopathic inhibiting effect on other algae, as described by Tassigny and Lefèvre (1971).

Our second and third hypothesis were based on expectations how changes in water turbulence might affect algal groups of different motility. With calming winds we expected to see less meroplanktonic species mechanically entrained into the planktonic compartment but more flagellates that would get an advantage during thermal stratification episodes in summer. Although the benthic diatoms were more abundant in the windier Period 2, their correlation with Shear3D remained nonsignificant and likely some other factors were responsible. The strong negative correlation of flagellated algae with Shear3D (Table 2) could be one of the direct expressions of wind effects on phytoplankton community composition. As our previous study (Woolway et al. 2017) showed, decreasing wind speeds have resulted in substantial changes in Võrtsjärv stratification dynamics, while increasing air temperature had a negligible effect. During stratification, a strong vertical turbulence gradient is formed, keeping the epilimnion mixed but attenuating in the meta- and hypolimnion. A modeling study of a stratified turbulent environment (Ross and Sharples 2008) showed that turbulence facilitates the large scale transport of cells within the turbulence gradient, but motility is the crucial factor that allows the cells to choose whether to stay in the mixing zone or swim away from it, optimizing by this their light and nutrient supply.

Despite a continuous decline in nutrient concentrations, the concentrations of Chl-*a* and TSS increased since 1996 when a considerable and rather abrupt decrease in wind speeds and a shorter wind fetch contributed to the decrease in bottom shear stress. The hypothetical mechanism explaining this contradiction by stimulated growth of light-limited phytoplankton is given in the conceptual diagram (Fig. 10).

Our study showed a dominating effect of WL over wind and shear stress on phytoplankton biomass and OAS concentrations

that can be explained by the different dynamic character of these forcing factors. However, as there was no significant difference in the mean WL before and after the onset of wind stilling, the 1.4-fold weaker average bottom shear stress, less frequently exceeding the critical threshold of 0.05 N m^{-2} , should have resulted in less suspended sediments in the water and a higher water transparency. Decreased external nutrient load and lower P release from sediment disturbance should have contributed to this trend by controlling P-limited phytoplankton growth. As no increase in water transparency was observed and the Limnothrix biomass increased, the compensatory growth of light-limited phytoplankton is the one plausible explanation. Therefore, the additional "light niche" caused by less suspended sediments in the water column would support phytoplankton growth until its increasing biomass compensates the TSS decrease and the self-shading returns light-limitation, closing the "light niche." Essentially the phytoplankton biomass increase counter-balances the lower bottom sediment resuspension, and the net effect is no improvement in water transparency. The increasing species richness during the atmospheric stilling period suggests that the light niche was capitalized by numerous species, however, L. planktonica took the most advantage, probably due to a combination of traits common to Oscillatoriales. These include high photosynthetic efficiency in dim light (Meffert 1989; Reynolds 1994), high P use efficiency resulting in more turbidity and shade created per unit of P than by other algae (Scheffer et al. 1997), and use of specific allelochemicals to suppress competitors (Tassigny and Lefèvre 1971). This mechanism explaining cyanobacteria development in stilling conditions has some common features with the one described by Posch et al. (2012) in which high N:P ratio and reduced water turnover in a deep lake allowed another filamentous cyanobacterium Planktothrix rubescens to accumulate within the depth of optimal irradiance. In a shallow lake (Taihu) Wu et al. (2016) found that calm weather supported the formation of Microcystis bloom by allowing the buoyant colonies to float and accumulate in the surface layer. These two mechanisms, however, are based on redistribution of the biomass rather than growth stimulation and differ principally from the one described in this study.

The replacement of declining amounts of suspended sediments by phytoplankton biomass was evidenced by two analyses: (1) the modeled relative share of OAS showed an increasing role of Chl-*a* against a decreasing role of TSS in total light attenuation in the stilling period and (2) the ratio of Phaeo to Chl-*a*, used as a marker for suspended sediments, showed constantly low values and decreased variability after 1996.

Conclusions

Our decadal scale time series revealed an abrupt 30% decrease in wind speed and change in wind direction since 1996 shortening the wind fetch in a large shallow temperate lake Võrtsjärv (Estonia). Combined, the 47% decrease in bottom shear stress should have increased water transparency. This, however, was not observed due to the compensatory growth of low-light adapted phytoplankton that capitalized on the "light niche" resulting from less sediment resuspension after the wind stilling.

The phytoplankton community composition revealed three distinct time periods, split by an increase in the WL from 1977 to 1979, and wind stilling since 1996. These environmental changes shifted the competitive advantage from *r*-selected coccal and colonial green algae and cyanobacteria to *K*-selected phytoplankton groups, dominated by shade adapted thin filamentous cyanobacteria from the genus *Limnotrhrix*.

Our study provides a plausible explanation to the counterintuitive empirical evidence of increased algal biomass against the background of decreasing nutrient concentrations, and continuously high water turbidity despite a drop in wind speed. If the mechanism is general in shallow lakes, wind stilling is another global factor complementing climate warming to reinforce eutrophication phenomena in lakes and postponing the achievement of the management targets set for the improvement of ecological status.

References

- Åberg, B., and W. Rodhe. 1942. Über die Milieufaktoren in einigen südschwedischen Seen. Acta Universitatis Upsaliensis.
- Baranowski, R., and Fryzlewicz, P. 2014. wbs: Wild Binary Segmentation for multiple change-point detection, 2014. R Package Version, 1.
- Bichet, A., M. Wild, D. Folini, and C. Schär. 2012. Causes for decadal variations of wind speed over land. Sensitivity studies with a global climate model. Geophys. Res. Lett. 39: L11701. doi:10.1029/2012GL051685
- Bormans, M., B. Maršálek, and D. Jančula. 2016. Controlling internal phosphorus loading in lakes by physical methods to reduce cyanobacterial blooms. A review. Aquatic Ecology 50: 407–422. doi:10.1007/s10452-015-9564-x
- Edler, L. 1979. Phytoplankton and chlorophyll: Recommendations on methods for marine biological studies in the Baltic Sea, p. 1–38. Baltic Marine Biologists Publication, v. **5**: 1–38.
- Emanuel, K. 2005. Increasing destructiveness of tropical cyclones over the past 30 years. Nature **436**: 686–688. doi: 10.1038/nature03906
- Fryzlewicz, P. 2014. Wild binary segmentation for multiple change-point detection. Ann. Statistics 42: 2243–2281. doi: 10.1214/14-AOS1245
- Gibson, C. E. 1987. Adaptations in Oscillatoria redekei at very slow growth rates—Changes in growth efficiency and phycobilin complement. Br. Phycol. J. **22**: 187–191. doi:10. 1080/00071618700650231
- Gkelis, S., P. Rajaniemi, E. Vardaka, M. Moustaka-Gouni, T. Lanaras, and K. Sivonen. 2005. Limnothrix redekei (Van Goor) Meffert (cyanobacteria) strains from Lake Kastoria, Greece form a separate phylogenetic group. Microb. Ecol. 49: 176–182.

- Guo, H., M. Xu, and Q. Hu. 2011. Changes in near-surface wind speed in China. 1969–2005. Int. J. Climatol. **31**: 349–358. doi:10.1002/joc.2091
- Håkanson, L. 1977. The influence of wind, fetch, and water depth on the distribution of sediments in Lake Vänern, Sweden. Can. J. Earth Sci. **14**: 397–412. doi:10.1139/e77-040
- He, J., and B. J. Soden. 2015. Anthropogenic weakening of the tropical circulation. The relative roles of direct CO_2 forcing and sea surface temperature change. J. Climate **28**: 8728–8742. doi:10.1175/JCLI-D-15-0205.1
- Holmroos, H., J. Niemistö, K. Weckström, and J. Horppila. 2009. Seasonal variation of resuspension-mediated aerobic release of phosphorus. Boreal Environ. Res. 14: 937–946.
- Idrizaj, A., A. Laas, U. Anijalg, and P. Nõges. 2016. Horizontal differences in ecosystem metabolism of a large shallow lake. J. Hydrol. 535: 93–100.
- Jaagus, J., and A. Kull. 2011. Changes in surface wind directions in Estonia during 1966-2008 and their relationships with large-scale atmospheric circulation. Est. J. Earth Sci. 60: 220–231.
- Jeffrey, S. W., and G. F. Humphrey. 1975. New spectrophotometric equations for determining chlorophylls a, b, c1 and c2 in higher plants, algae and natural phytoplankton. Biochemie und Physiologie der Pflanzen **167**: 191–194. doi:10. 1016/S0015-3796(17)30778-3
- Kallio, K., J. Pulliainen, and P. Ylöstalo. 2005. MERIS, MODIS and ETM+ channel configurations in the estimation of lake water quality from subsurface reflectance using semianalytical and empirical algorithms. Geophysica **41**: 31–55.
- Kirk, J. T. O. 1994. Light and photosynthesis in aquatic ecosystems. Cambridge Univ. Press.
- Klink, K. 1999. Trends in mean monthly maximum and minimum surface wind speeds in the coterminous United States, 1961 to 1990. Climate Res. **13**: 193–205.
- Kragh, T., K. Sand-Jensen, K. Petersen, and E. Kristensen. 2017. Fast phosphorus loss by sediment resuspension in a re-established shallow lake on former agricultural fields. Ecol. Eng. **108**: 2–9.
- Laas, A., P. Nõges, T. Kõiv, and T. Nõges. 2012. High-frequency metabolism study in a large and shallow temperate lake reveals seasonal switching between net autotrophy and net heterotrophy. Hydrobiologia **694**: 57–74. doi:10.1007/s10750-012-1131-z
- Legendre, P., and L. Legendre. 1998. Numerical ecology, volume 24, (developments in environmental modelling). The Netherlands: Elsevier Science Amsterdam.
- Lorenzen, C. J. 1967. Determination of chlorophyll and pheopigments. Spectrophotometric equations 1. Limnol. Oceanogr. 12: 343–346.
- Lu, J., G. A. Vecchi, and T. Reichler. 2007. Expansion of the Hadley cell under global warming. Geophys. Res. Lett. 34: L06805. doi:10.1029/2006GL028443
- Luettich, R. A., Jr., D. R. Harleman, and L. Somlyody. 1990. Dynamic behavior of suspended sediment concentrations

in a shallow lake perturbed by episodic wind events. Limnol. Oceanogr. **35**: 1050–1067.

- MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton: Princeton Univ. Press.
- Magee, M. R., and C. H. Wu. 2017. Response of water temperatures and stratification to changing climate in three lakes with different morphometry. Hydrol. Earth Syst. Sci. **21**: 6253–6274. doi:10.5194/hess-21-6253-2017
- McVicar, T. R., and M. L. Roderick. 2010. Atmospheric science: Winds of change. Nature Geosci. **3**: 747–748.
- McVicar, T. R., and others. 2012. Global review and synthesis of trends in observed terrestrial near-surface wind speeds: Implications for evaporation. J. Hydrol. **416-417**: 182–205. doi:10.1016/j.jhydrol.2011.10.024
- Meffert, M. E. 1989. Planktic unsheated filaments (Cyanophyceae) with polar and central gas vacuoles. II. Biology, population dynamics and biotopes of Limnothrix redekei (Van Goor) Meffert. Archiv für Hydrobiologie **116**: 257–282.
- Nõges, P. 2000. Euphotic holding capacity for optically active substances. Geophysica **36**: 169–176.
- Nõges, P., and A. Järvet. 1995. Water level control over light conditions in shallow lakes. Report Series in Geophysics, University of Helsinki **32**: 81–92.
- Nõges, P., and T. Nõges. 1998. The effect of fluctuating water level on the ecosystem of Lake Võrtsjärv, Central Estonia. Proc. Estonian Acad. Sci. Biol. Ecol 47: 98–113.
- Nõges, P., and T. Nõges. 2012. Võrtsjärv Lake in Estonia, p. 850–861. *In* L. Bengtsson, R. W. Herschy, and R. W. Fairbridge [eds.], Encyclopedia of lakes and reservoirs. Netherlands: Springer.
- Nõges, P., and T. Nõges. 2014. Weak trends in ice phenology of Estonian large lakes despite significant warming trends. Hydrobiologia **731**: 5–18. doi:10.1007/s10750-013-1572-z
- Nõges, P., and L. Tuvikene. 2012. Spatial and annual variability of environmental and phytoplankton indicators in Lake Võrtsjärv: Implications for water quality monitoring. Est. J. Ecol. **61**: 227–246.
- Nõges, P., U. Mischke, R. Laugaste, and A. G. Solimini. 2010. Analysis of changes over 44 years in the phytoplankton of Lake Võrtsjärv (Estonia). The effect of nutrients, climate and the investigator on phytoplankton-based water quality indices. Hydrobiologia **646**: 33–48. doi:10.1007/s10750-010-0178-y
- Nõges, T., and P. Nõges. 1999. The effect of extreme water level decrease on hydrochemistry and phytoplankton in a shallow eutrophic lake, p. 277–283. *In* N. Walz and B. Nixdorf [eds.], Shallow Lakes '98: Trophic interactions in shallow freshwater and brackish waterbodies. Netherlands: Springer.
- Paavel, B., K. Kangro, H. Arst, A. Reinart, T. Kutser, and T. Nõges. 2016. Parameterization of chlorophyll-specific phytoplankton absorption coefficients for productive lake waters. J. Limnol. **75**: 423–438.
- Papanikolopoulou, L. A., E. Smeti, D. L. Roelke, P. G. Dimitrakopoulos, G. D. Kokkoris, D. B. Danielidis, and S.

Spatharis. 2018. Interplay between r- and K-strategists leads to phytoplankton underyielding under pulsed resource supply. Oecologia **186**: 755–764. doi:10.1007/s00442-017-4050-x

- Pirazzoli, P. A., and A. Tomasin. 2003. Recent near-surface wind changes in the Central Mediterranean and Adriatic areas. Int. J. Climatol. 23: 963–973. doi:10.1002/joc.925
- Posch, T., O. Köster, M. M. Salcher, and J. Pernthaler. 2012. Harmful filamentous cyanobacteria favoured by reduced water turnover with lake warming. Nat. Clim. Change **2**: 809–813. doi:10.1038/nclimate1581
- Ramette, A. 2007. Multivariate analyses in microbial ecology. FEMS Microbiol. Ecol. **62**: 142–160.
- Raukas, A. 2004. Bottom deposits, p. 79–86. *In* J. Haberman, E. Pihu, and A. Raukas [eds.], Lake Võrtsjärv. Tallinn: Estonian Encyclopedia Publishers.
- Reinart, A., and P. Nõges. 2004. Light condition in lake Võrtsjärv, p. 141–149. *In* Võrtsjärv. Estonian: Encyclopedia Publishers.
- Reynolds, C. S. 1994. The long, the short and the stalled: On the attributes of phytoplankton selected by physical mixing in lakes and rivers. Hydrobiologia **289**: 9–21. doi:10.1007/BF00007405
- Roderick, M. L., L. D. Rotstayn, G. D. Farquhar, and M. T. Hobbins. 2007. On the attribution of changing pan evaporation. Geophys. Res. Lett. **34**: L17403. doi:10.1029/ 2007GL031166
- Ross, O. N., and J. Sharples. 2008. Swimming for survival: A role of phytoplankton motility in a stratified turbulent environment. J. Marine Syst. **70**: 248–262. doi:10.1016/j. jmarsys.2006.07.008
- Rücker, J., J.-G. Kohl, and K. Kaiser. 1995. Responses of carotenoids and chlorophylls to variations of growth-limiting factors in three filamentous blue-green algae. Algological Studies/Archiv für Hydrobiologie, Supplement volumes **77**: 51–65.
- Schallenberg, M., and C. W. Burns. 2004. Effects of sediment resuspension on phytoplankton production. Teasing apart the influences of light, nutrients and algal entrainment. Freshwater Biol. **49**: 143–159. doi:10.1046/j.1365-2426. 2003.01172.x
- Scheffer, M., S. Rinaldi, A. Gragnani, L. R. Mur, and E. H. van Nes. 1997. On the dominance of filamentous cyanobacteria in shallow, turbid lakes. Ecology 78: 272–282. doi:10.1890/ 0012-9658(1997)078[0272:OTDOFC]2.0.CO;2
- Sharma, S., D. A. Swayne, and C. Obimbo. 2016. Trend analysis and change point techniques. A survey. Energy. Ecol. Env. 1: 123–130. doi:10.1007/s40974-016-0011-1
- Sheng, Y., and W. Lick. 1979. The transport and resuspension of sediments in a shallow lake. J. Geophys. Res. **84**: 1809–1826. doi:10.1029/JC084iC04p01809
- Sheng, Y. P., D. E. Eliason, R. E. Dickinson, and J. K. Choi. 1991. A three-month simulation of wind-driven circulation, sediment transport, and phosphorus transport in

Lake Okeechobee. Coastal & Oceanographic Engineering Department, Rep. 91-023. Gainesville: University of Florida.

- Tassigny, M., and M. Lefèvre. 1971. Auto., hétéroantagonisme et autres conséquences des excrétions d'algues d'eau douce ou thermale. SIL Commun., 1953-1996 **19**: 26–38. doi:10. 1080/05384680.1971.11903921
- Timm, T. [ed.]. 1973. Võrtsjärv. Tallinn: Valgus, p. 284.
- Tuller, S. E. 2004. Measured wind speed trends on the west coast of Canada. Int. J. Climatol. 24: 1359–1374. doi:10. 1002/joc.1073
- Tuvikene, L., T. Nõges, and P. Nõges. 2011. Why do phytoplankton species composition and "traditional" water quality parameters indicate different ecological status of a large shallow lake? Hydrobiologia **660**: 3–15. doi:10.1007/ s10750-010-0414-5
- Utermöhl, H. 1958. Methods of collecting plankton for various purposes are discussed. SIL Commun., 1953-1996 **9**: 1–38. doi:10.1080/05384680.1958.11904091
- Vautard, R., J. Cattiaux, P. Yiou, J.-N. Thépaut, and P. Ciais. 2010. Northern Hemisphere atmospheric stilling partly attributed to an increase in surface roughness. Nat. Geosci. 3: 756.
- Walker, T. R., J. Grant, P. Cranford, D. G. Lintern, P. Hill, P. Jarvis, J. Barrell, and C. Nozais. 2008. Suspended sediment and erosion dynamics in Kugmallit Bay and Beaufort Sea during ice-free conditions. J. Mar. Syst. 74: 794–809.
- Walsby, A. E. 2005. Stratification by cyanobacteria in lakes: A dynamic buoyancy model indicates size limitations met by *Planktothrix rubescens* filaments. New Phytol. **168**: 365–376. doi:10.1111/j.1469-8137.2005.01508.x
- Wang, H., Z. Zhang, D. Liang, H. Du, Y. Pang, K. Hu, and J. Wang. 2016. Separation of wind's influence on harmful cyanobacterial blooms. Water Res. 98: 280–292. doi:10. 1016/j.watres.2016.04.037
- Wilhelm, S., and R. Adrian. 2008. Impact of summer warming on the thermal characteristics of a polymictic lake and consequences for oxygen, nutrients and phytoplankton. Freshwater Biol. **53**: 226–237. doi:10.1111/j.1365-2427.2007. 01887.x
- Woolway, R. I., and J. H. Simpson. 2017. Energy input and dissipation in a temperate lake during the spring transition. Ocean Dynam. **67**: 959–971. doi:10.1007/s10236-017-1072-1
- Woolway, R. I., P. Meinson, P. Nõges, I. D. Jones, and A. Laas. 2017. Atmospheric stilling leads to prolonged thermal stratification in a large shallow polymictic lake. Clim. Change 141: 759–773. doi:10.1007/s10584-017-1909-0
- Woolway, R. I., and others. 2018. Geographic and temporal variations in turbulent heat loss from lakes: A global analysis across 45 lakes. Limnol. Oceanogr. **63**: 2436–2449.
- Wu, J., J. Zha, D. Zhao, and Q. Yang. 2018. Changes in terrestrial near-surface wind speed and their possible causes. An

overview. Climate Dynam. **51**: 2039–2078. doi:10.1007/s00382-017-3997-y

- Wu, T., B. Qin, J. D. Brookes, K. Shi, G. Zhu, M. Zhu, W. Yan, and Z. Wang. 2015. The influence of changes in wind patterns on the areal extension of surface cyanobacterial blooms in a large shallow lake in China. Sci. Total Environ. **518-519**: 24–30. doi:10.1016/j.scitotenv. 2015.02.090
- Wu, T., H. Timo, B. Qin, G. Zhu, R. Janne, and W. Yan. 2016. In-situ erosion of cohesive sediment in a large shallow lake experiencing long-term decline in wind speed. J. Hydrol. 539: 254–264. doi:10.1016/j.jhydrol.2016.05.021
- Xu, M., C.-P. Chang, C. Fu, Y. Qi, A. Robock, D. Robinson, and H.-m. Zhang. 2006. Steady decline of east Asian monsoon winds, 1969–2000. Evidence from direct ground measurements of wind speed. J. Geophys. Res. **111**: D24111. doi:10.1029/2006JD007337

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Conflict of Interest

None declared.

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