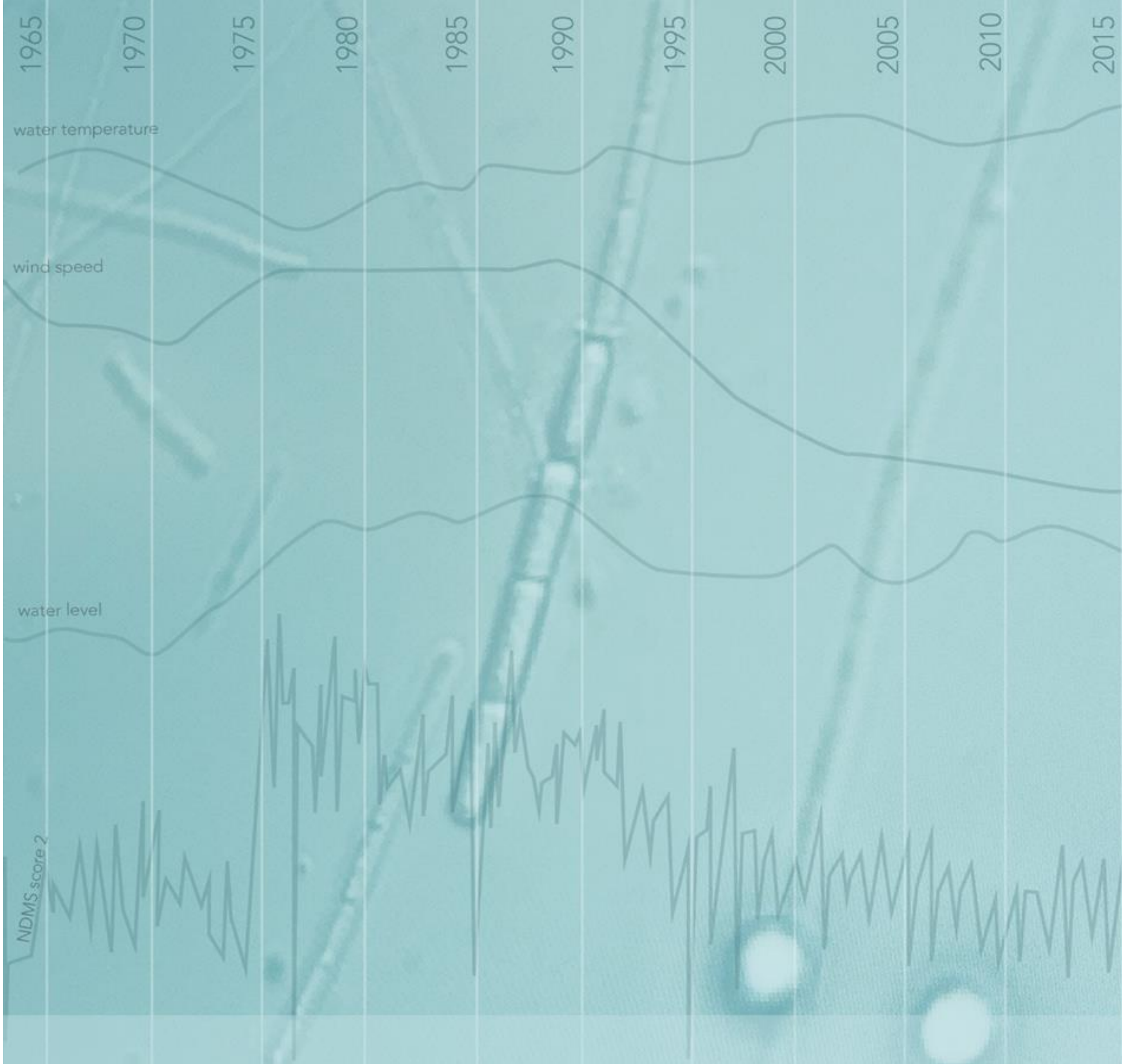
Hydrometeorological and climatic control over lake phytoplankton: the importance of time scales

Nasime Janatian



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Nasime Janatian Ghadikolaei

Tartu, 2021

UNIVERSITAT DE BARCELONA

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Hüdrometeoroloogiliste ja kliimategurite mõju järvede fütoplanktonile: ajaskaalade olulisus

Thesis for applying for the degree of Doctor of Philosophy

in Environmental Sciences and Applied Biology

Väitekiri

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Thesis for applying for the degree of Doctor of Philosophy in Ecology, Environmental Sciences and Plant Physiology

Nasime Janatian

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Approval of Thesis supervisors

Dr. Peeter Nõges Dr. Biel Obrador

Dr. Alo Laas Dr. Fabien Cremona

Wisdom sails with wind and time.

___ John Florio

Dedicated to my parents, the best auntie ever, Afsaneh and

my beloved siblings Nima, Navid & Negin

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Supervisors’ report

Dr. Peeter Nõges, Leading Researcher, Dr. Alo Laas, Senior Researcher, and Dr. Fabien Cremona, Senior Researcher at the Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, and Dr. Biel Obrador Sala, Associate Professor at the Department of Evolutionary Biology, Ecology and Environmental Sciences of the University of Barcelona, as supervisors of the PhD thesis entitled “Hydrometeorological and climatic control over lake phytoplankton: the importance of time scales",

REPORT

that the research developed by Nasime Janatian Ghadikolaei in her Doctoral Thesis has resulted in three scientific publications already published:

Stockwell, J.D., Doubek, J.P., Adrian, R., Anneville, O., Carey, C.C., Carvalho, L., De Senerpont Domis, L.N., Dur, G., Frassl, M.A., Grossart, H.-P., Ibelings, B.W., Lajeunesse, M.J., Lewandowska, A.M., Llames, M.E., Matsuzaki, S.S., Nodine, E.R., Nõges, P., Patil, V.P., Pomati, F., Rinke, K., Rudstam, L.G., Rusak, J.A., Salmaso, N., Seltmann, C.T., Straile, D., Thackeray, S.J., Thiery, W., Urrutia-Cordero, P., Venail, P., Verburg, P., Woolway, R.I., Zohary, T., Andersen, M.R., Bhattacharya, R., Hejzlar, J., **Janatian, N.,** Kpodonu, A.T.N.K., Williamson, T.J., Wilson, H.L. 2020. Storm Impacts on Phytoplankton Community Dynamics in Lakes. Global Change Biology 26(5): 2756-2784. https://doi.org/10.1111/gcb.15033

> The 2019 Journal Impact Factor of *Global Change Biology* in Web of Science was 8.555. The journal is ranked in Q1 in the categories *BIODIVERSITY CONSERVATION, ECOLOGY* and *ENVIRONMENTAL SCIENCES.*

Janatian, N., Olli, K., Cremona, F., Laas, A. & Nõges, P. 2020. Atmospheric stilling offsets the benefits from reduced nutrient loading in a large shallow lake. Limnology and Oceanography 65(4), 717-731.

> The 2019 Journal Impact Factor of *Limnology and Oceanography* in Web of Science was 3.778. The journal is ranked in Q1 in the categories *LIMNOLOGY* and *OCEANOGRAPHY*.

Janatian, N., Olli, K. & Nõges, P. 2021. Phytoplankton responses to meteorological and hydrological forcing at decadal to seasonal time scales. Hydrobiologia (accepted 13.04.21) https://doi.org/10.1007/s10750-021-04594-x

> The 2019 Journal Impact Factor of Hydrobiologia in Web of Science was 2.385. The journal is ranked in Q1 in the category *MARINE & FRESHWATER BIOLOGY*.

We also certify that Nasime Janatian Ghadikolaei has actively participated in all research tasks involved in these publications: setting the objectives and developing the research hypotheses, conceiving and performing the data handling and statistical analyses, analysing the results, and writing the manuscripts.

Finally, we certify that none of the co-authors of the publications that conform this doctoral thesis, has used or will use these results as part of any other PhD thesis.

Tartu, 2nd June 2021

Dr. Peeter Nõges

Dr. Biel Obrador

P. Nõges

Dr. Fabien Cremona
Dr. Alo Laas

The English and Estonian in the current thesis was edited by Peeter Nõges, PhD.

CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, referred to in the text by the relevant Roman numerals. Papers are reproduced by the kind permission from the publishers.

I. Stockwell, J.D., Doubek, J.P., Adrian, R., Anneville, O., Carey, C.C., Carvalho, L., De Senerpont Domis, L.N., Dur, G., Frassl, M.A., Grossart, H.-P., Ibelings, B.W., Lajeunesse, M.J., Lewandowska, A.M., Llames, M.E., Matsuzaki, S.S., Nodine, E.R., Nõges, P., Patil, V.P., Pomati, F., Rinke, K., Rudstam, L.G., Rusak, J.A., Salmaso, N., Seltmann, C.T., Straile, D., Thackeray, S.J., Thiery, W., Urrutia-Cordero, P., Venail, P., Verburg, P., Woolway, R.I., Zohary, T., Andersen, M.R., Bhattacharya, R., Hejzlar, J., **Janatian, N.,** Kpodonu, A.T.N.K., Williamson, T.J., Wilson, H.L. 2020. Storm Impacts on Phytoplankton Community Dynamics in Lakes. Global Change Biology 26(5): 2756-2784. https://doi.org/10.1111/gcb.15033

II. Janatian, N., Olli, K., Cremona, F., Laas, A. & Nõges, P. 2020.Atmospheric stilling offsets the benefits from reduced nutrient loading in a large shallow lake. Limnology and Oceanography 65(4), 717-731.

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CONTRIBUTIONS

	I	II	III
Idea	Stockwell et al.	**NJ**, PN, KO	**NJ,** PN
Data collection	**NJ**, Stockwell et al.	PN	PN
Data analyses	Stockwell et al.	**NJ**, PN	**NJ**, PN, KO
Manuscript preparation	**NJ**, Stockwell et al.	PN, **NJ**, FC, AL, KO	PN**, NJ**, KO
NJ- Nasime Janatian; PN- Peeter Nõges; FB- Fabien Cremona; AL- Alo Laas; KO- Kalle Olli			

ABBREVIATIONS

C’	Specific attenuation coefficient
CDOM	Colored dissolved organic matter
Chl-a	Chlorophyll-a
ENSO	El Niño-Southern Oscillation
EWEs	Extreme weather events
GAM	Generalised additive models
k_W	Attenuations caused by pure water
NAO	North Atlantic Oscillation
NMDS	Nonmetric Multidimensional Scaling
OAS	Optically active substances
P	Phosphorus
PAR_0	Photosynthetically active radiation
PAR_{mix}	The mean PAR within the mixed layer
SD	Secchi depth

SWT	Surface water temperature
TSS	Total suspended solids
U	Wind speed at 10 m height
WA: LSA	The watershed area to lake surface area ratio
WBS	Wild binary segmentation
WL	Lake water levels
z_{eu}	Euphotic depth
z_{mix}	Mixing depth

1 INTRODUCTION

In most aquatic ecosystems, phytoplankton forms the foundation of the food chain, which provides newly produced organic matter to the higher trophic levels and, ultimately, supports the fisheries that millions of people rely on for food (Mooij et al., 2005; Watson et al., 2013; M Winder & Sommer, 2012). Phytoplankton organisms have global impacts also on biogeochemical cycles and the climate system (Wang et al., 2018). While freshwater ecosystems cover only 2.3% of the Earth’s surface, these ecosystems host a manifold larger proportion of the Earth’s biodiversity (Reid et al., 2019). High biodiversity and fast reaction to environmental changes make freshwater phytoplankton a valuable status indicator in aquatic ecosystems monitoring (Phillips et al., 2013) and planning lake management strategies (Nõges et al., 2020; Urrutia-Cordero et al., 2016). On the other hand, cyanobacteria in lakes and reservoirs form harmful blooms that with their toxicity represent a vast risk for human health and safe drinking water supply (Brooks et al., 2016). Taken together, a greater understanding of the community ecology of lake phytoplankton has a direct outcome for studying complex lake ecosystem processes. To optimize lake management and anticipate bloom formation, it is increasingly vital to understand these organisms and complex mechanisms that shape their communities over different time scales (Mooij et al., 2010).

Phytoplankton dynamics depends largely on availability of light and nutrient resources that support growth, and infections, grazing pressure, and sedimentation that cause losses in the community. Hydro-meteorological and climatic conditions modify these direct environmental factors determining what kind of phytoplankton develops at variable spatial and temporal scales (M Winder & Sommer, 2012). Recently, the impacts of extreme climatic events on lakes and phytoplankton dynamics have received further attention in a substantial body of research (Jennings et al., 2012).

The pace of global environmental change due to ongoing global warming is predicted to have profound consequences, such as increasing the occurrence of extreme weather events (EWEs) (Jeppesen et al., 2021). EWEs include e.g., heat waves, windstorms, long calm periods (atmospheric stilling), droughts, and sudden severe rainfalls. Lake researchers generally identify the extremes in climate and hydrological datasets using thresholds connected to observed data (Seneviratne et al., 2012). Although the values will vary based on location and the local climate, thresholds related to local meteorological data have been used to define possible EWEs within lakes (e.g., Perga et al., 2018). EWEs and changes in their frequency, duration, and intensity threaten ecological and evolutionary processes of lakes, affecting their structure and functioning (e.g., Gao et al., 2021; Jeppesen et al., 2021; Woolway et al., 2021). However, Jeppesen et al. (2021) highlighted that there is no universally accepted approach to identify the extreme events for lake-related studies, and that not all extreme forcing events are biologically impactful. According to their review, a wealth of new environmental observations is coming up with recent advances in real-time high-resolution monitoring resulting from an upward trend in implementing in-situ monitoring platforms in a large number of lakes across the globe. This new data may shed light on even short-term effects of EWEs in different lakes with various local climates. Nevertheless, to understand the functioning and dynamics of the phytoplankton community of lakes, we must understand how the timing, intensity, and duration of the local forcing factors can influence the system.

A variety of hydrometeorological factors and mechanisms compete to control the dynamics of the phytoplankton community (Rohr et al., 2017). It complicates drawing direct causality to figure out why and how phytoplankton communities form and change. Because the phytoplankton community contains species representing different life strategies (e.g., opportunistic vs. tolerant species) and variously adapted to changes in the environment, they perceive disturbances related to highly variable hydrometeorological and climatic control differently at various time scales (Wu et al., 2013). Among this variety of hydrometeorological forcing factors, wind speed is one of the most influential climatic driver of the lake's physical processes and, consequently, phytoplankton dynamics (Woolway et al., 2019; Wuest & Lorke, 2003). A wind event, for example, may disrupt cyanobacteria surface bloom (Wu et al., 2013) but give an advantage to diatoms that need higher turbulence or green algae by creating a nutrient pulse through deeper mixing (Carrick et al., 1993). Short-term responses of phytoplankton to stochastic disturbances by wind are likely to constitute a large part of the total variability in phytoplankton (Kasprzak et al., 2017).

Numerous studies using wind databases have revealed globally how fickle wind can be. Over the same period, in one part of the globe the wind is blowing intensively with an upward trend in intensity, frequency, and storm duration (Lehmann et al., 2015; Zhang et al., 2013) , while the other parts are still (Bichet et al., 2012; Vautard et al., 2010; Woolway et al., 2019). In recent decades, average wind speeds tend to decrease by 0.11 m s^{-1} per decade across several sites (Vautard et al., 2010). Remarkably, this is nearly indistinguishable from the trends reported in many other regions over the globe (McVicar & Roderick, 2010; Pryor et al., 2009; Roderick et al., 2007; Zheng et al., 2009). Until recently, most limnologists have ignored stilling influence as a new climatic challenge in climate change assessments and studies on lakes, owing to an implicit assumption that surface air temperature is the critical factor causing lake responses to climate change (O’Reilly et al., 2015; Wang et al., 2018; Winslow et al., 2018).

In the present thesis we focus on the two extremes of the wind speed – storms and atmospheric stilling – and analyse their impacts on lake environments and phytoplankton dynamics over short and long periods. As we realised the importance of the time scale in the context of our wind effect studies, we decided to have a closer look at other environmental data in the Lake Võrtsjärv database addressing the questions how the variability in environmental factors (thermal, wind, light- and water-level regimes) and phytoplankton variables is partitioned among different time scales from days to decades and whether matching shares can help to determine the leading factors responsible for phytoplankton dynamics.

2 REVIEW OF THE LITERATURE

2.1 Factors controlling phytoplankton: specific features of lakes

Phytoplankton collectively contributes about half of the global organic matter production (Boyce et al., 2010). Despite small individual sizes, and sometimes low total biomass (Dröscher et al., 2009), phytoplankton fuels the entire aquatic food web. With eutrophication pressure exceeding planetary boundaries and becoming a major threat to biosphere integrity in both fresh and marine waters worldwide (Steffen et al., 2015), the role of nutrients controlling phytoplankton biomass and community composition has been recognised and thoroughly studied for years. Still the validity of the N:P stoichiometric concept as the mechanism controlling cyanobacterial blooms (Smith, 1990) is continuously debated (Chorus & Spijkerman, 2021; Howarth & Paerl, 2008; Le Moal et al., 2019; Schindler & Hecky, 2008). Increasing N and P loads with eutrophication lead to biomass growth and self-shading of the phytoplankton shifting the competition from nutrients to light (Burson et al., 2018) that is the third most common limiting factor for phytoplankton in the "nutrient-load hypothesis". Other frequently discussed limiting factors of phytoplankton include dissolved inorganic carbon (Riebesell & Wolf-Gladrow, 2002), iron (Hoffmann et al., 2007), silicon (Parker et al., 1977), and bioactive trace metals (McKay et al., 2001). Although continuous progress has made to understand the effects of both abiotic (e.g., Cuypers et al., 2011; Durham et al., 2013; Posch et al., 2012) and biotic factors (e.g., Amin et al., 2015; Eiler et al., 2012; Shatwell et al., 2016) in phytoplankton ecology, many authors admit that the mechanisms controlling phytoplankton community composition and dynamics still remain poorly understood. An unexhaustive list of the reasons for that includes:

- nonlinearities in the atmosphere–hydrosphere–biosphere relationships (Francis et al., 1998),

- the dynamic balance between bottom-up and top-down control mechanisms of phytoplankton (Shurin et al., 2012),
- interactions between multiple forcing factors in aquatic environments (Nõges et al., 2016),
- the dual nature of community variability: compositional vs. aggregate variation (Micheli et al., 1999),
- the lack of consistent phytoplankton data to quantify and understand the causes of long-term trends (Siegel & Franz, 2010).

According to Li et al. (2010), one of the main reasons adding uncertainty to phytoplankton models is the frequently overlooked multiscalarity issue arising from the spatially and temporally different linkages between hydrometeorological and biological responses, playing a critical role in knowledge-based water and lake management studies.

Lakes contain 68% of the global liquid surface freshwater (Beeton, 2002) and are highly diverse in their chemical, physical, and biological characteristics that constantly influence their ecosystems. Further, lakes can be shallow or deep, permanent, or temporary, and contain fresh or salty water (in dry regions). The size of lakes follows the Pareto distribution meaning that there are millions of small lakes compared to the small number of large lakes (>= 500 km^2) globally (Downing et al., 2006).

At even short distances from each other, lakes can exhibit highly distinct and unique phytoplankton communities depending on differences in the lake area, nutrient concentration, mixing regime, and other so-called environmental filters (Stomp et al., 2011; Xiao et al., 2016). At the same time, similar lakes at considerable distances may have somewhat similar phytoplankton, at least at conventional taxonomic resolution. Consequently, the role of environmental filters in shaping phytoplankton community composition and dynamics in individual lakes remains undisputable and enables using phytoplankton in lake typology (Borics et al., 2014) and ecological status assessment (Lepistö et al., 2004; Padisák et al., 2006). Besides abiotic factors such as nutrient availability, light conditions, and lake morphometry (Stomp et al., 2011), the biodiversity patterns in freshwater phytoplankton depend strongly on selective zooplankton grazing (Carpenter et al., 2010), competition with macrophytes (Muylaert et al., 2010), interactions with bacteria (Amin et al., 2015; Eiler et al., 2012), and viral control (Short et al., 2011). However, Hansson et al. (2013) demonstrated that community responses to global change in aquatic systems depend on food-chain length. The top trophic level and every second level below will tend to benefit from climate change, whereas the levels in between will suffer. Thus, numerous interactions and feedback mechanisms in lakes play an integral role in complicated phytoplankton control mechanisms.

2.2 Storm impacts and phytoplankton in lakes

According to exact meteorological expression, the term "storm" refers to “an atmospheric disturbance involving perturbations of the prevailing pressure and wind fields, on scales ranging from tornadoes (1 km across) to extratropical cyclones (2000–3000 km across)” and/or “wind with a speed between 48 and 55 knots (25 and 28 m/s; Beaufort scale wind force 10)” (World Meteorological Organization, 1967, p. 148).

Despite a slack in average wind speeds over several regions of the world in recent decades, the frequency, intensity, and period of storms have risen over the same period and are generally estimated to continue to increase (Lehmann et al., 2015; Zhang et al., 2013). Hence, even with a clear understanding of the change in lake physics, chemistry or biogeochemical processes caused by storms and linked precipitation (Znachor et al., 2008), the mechanisms behind the storm impacts on planktonic ecosystems are often only poorly understood. Biological responses to storms may be associated with one or more ecological organization levels, from individuals to ecosystems (Felton et al., 2017). In contrast, the time resolution of the response may be quick or slow (Giling et al., 2017), and the time scale may last from minutes to decades (Perga et al., 2018; Rusak et al., 2018). Kuha et al. (2016) demonstrated that because of the fast growth rate and short generation time, phytoplankton reacts rapidly to storm events in lakes with changes in diversity, community composition, and primary production. This rapid response alters the function and services of lake ecosystems. The authors explained that due to diverse taxonomy, the functional traits of algae and cyanobacteria become particularly important to cope with storm-induced changes in lakes because phytoplankton can respond rapidly to changes in significant growth determinants, i.e., light, nutrient, and temperature conditions.

Although storms clearly play an integral role in forming the phytoplankton community dynamics in lakes, this role is context-dependent; there remains a great deal of mystery surrounding what controls the variability of phytoplankton dynamics in relation to the environmental and ecological conditions of lakes. Here, we summarise our general and mechanistic understanding of how physical processes and possible impacts of storm-induced disturbances on phytoplankton dynamics could be utilised in a management-related framework that could be beneficial for future studies on wind and precipitation induced changes in the physical and chemical structure of the water column (i.e., light, temperature, and nutrients) and their expected impact on the dynamics of lake phytoplankton.

Shallow versus deep lakes are differently affected by wind, related to the different mixing depth to physical depth ratio (Delandmeter et al., 2018). Precipitation events and subsequent runoff and flushing have other influences in reservoirs, deep lakes, and shallow lakes linked to the differences in water residence times (Hayes et al., 2017) and the water layer toward which the inflow penetrates (Vilhena et al., 2010). By affecting cyanobacterial blooms, winds may also modify the manifestation of eutrophication phenomena. The impact of wind on harmful algal surface blooms can be divided into three components (Wang et al., 2016):

1. disturbance influence on cyanobacterial proliferation,
2. nutrient effect by sediment release, and
3. wind and wave-induced surface drift affected by transportation.

Further, the wind-induced sediment resuspension will affect the whole phytoplankton community through strengthened light attenuation and transport of meroplanktonic algae from the lakebed to the water column (Schallenberg & Burns, 2004). Given all the above-described effects that winds may have on phytoplankton, it is obvious that nullifying these effects by wind stilling will have an impact of a comparable magnitude.

2.3 The winds of change in Lake Võrtsjärv

Atmospheric stilling is a downward trend of near-surface (~10 m) terrestrial wind speed reported recently. This slowdown has had significant implications for many regions globally, including lakes in which it leads to substantial changes in thermal stratification and mixing dynamics. Although no single reason to explain atmospheric stilling has been found, some of the hypothesised drivers of this phenomenon are as follows (Woolway et al., 2019, 2020):

1. a decrease in the equatorial-polar thermal gradient,
2. shifts in mean circulation,
3. an enhancement in land-surface roughness.

The occurrence of atmospheric stilling in several regions of the world has been demonstrated in a review of 148 studies (Woolway et al., 2019). As one example, Woolway et al. (2017) illustrate a significant change in thermal stratification in a large shallow polymictic lake (Võrtsjärv) in Estonia due to the sudden decrease in surface wind speed since the mid-1990s, which led to a higher number of stratified days.

Furthermore, previous studies have distinguished the critical role of water level (WL) fluctuations in driving water quality in Võrtsjärv. Stronger sediment resuspension at low WLs leads to low water transparency due to enrichment with suspended solids. Paradoxically, the average light conditions in the water column improved because lower WL “cut off” less illuminated and less productive deeper layers (Nõges & Nõges, 1999).

Shade-adapted and low-temperature tolerant slow-growing cyanobacteria species from the order Oscillatoriales representing

K-strategists among phytoplankton (MacArthur & Wilson, 2016; Reynolds, 1996), dominate in Võrtsjärv. Until the end of the 1970s, *Planktolyngbya limnetica* (Lemm.) J. Komárková-Legnerova was the main dominant in Võrtsjärv, which thereafter was taken over by *Limnothrix redekei* (Goor) Meffert and *L. planktonica* (Wołosz.) Meffert, which now account for 60 to 90% of the total phytoplankton biomass. Diatoms are indicated as the second abundant group in Võrtsjärv, in which the majority of the biomass is formed by large filamentous *Aulacoseira* spp.

With its long uninterrupted hydro-meteorological and biological time-series covering more than half century (Nõges et al., 2001), Võrtsjärv provides a unique opportunity to study environmental impacts on a shallow lake ecosystem. Large area open to winds makes the lake highly sensitive to atmospheric drivers. In the light of recent discoveries on the changing wind pattern (Woolway et al., 2017) we expected to see an improvement of water transparency associated with reduced sediment disturbance.

2.4 Phytoplankton dynamics and the multiscalarity issue

Identification and evaluation of driving factors underlying dynamic patterns in community composition, diversity, and abundance form the essence of ecology (Thomas et al., 2018). Since Hutchinson’s work on the “paradox of the plankton” (1961) explaining why many phytoplankton species could co-exist on a limited number of resources, Tilman’s theoretical works on resource competition theory (1977; 1982), Reynolds' (1973) application of the intermediate disturbance hypothesis (Connell, 1978) into phytoplankton succession, and some fundamental studies on food-chain interactions (e.g. Leibold, 1996), no theoretical break-through in phytoplankton ecology of a similar magnitude has occurred. Although it is generally understood that nutrient loading and light drive phytoplankton blooms, the degree to which phytoplankton community composition and conditions are changing globally and the factors that drive these shifts among multiple interacting stressors the phytoplankton dynamic are still uncertain (Ho et al., 2021; Pahlevan et al., 2021).

The lack of information on temporal and spatial coupling between crucial physical, chemical, and biological drivers in phytoplankton models causes epistemic uncertainty in these models. Various phytoplankton species require resources in a unique combination based on their resource optima, evolutionary adaptations, and life strategies that cause their different reaction to disturbances (Reynolds, 2006; Istvánovics & Honti, 2021). Short-term responses to stochastic events form likely a large part of the total variability in phytoplankton (Kasprzak et al., 2017). Although wind events with a time scale of few days can increase the abundance of the largest-sized phytoplankton species more than the smallest ones, an enhancement in stratification has the opposite consequences (Pannard et al., 2007). The seasonal cycle of light and temperature makes an essential contribution to phytoplankton variability (Vallina et al., 2017). The impacts of anthropogenic eutrophication and changes in catchment land use acting at decadal to centennial time-scales have to be revisited in the light of their strong interaction with climate change (Moss et al., 2011).

Many studies have been dedicated to temporal dynamics of phytoplankton at time scales from geological to diurnal, but there is little information on cross-scale patterns (Li et al., 2010). In each of the time scales, the factors and mechanisms governing phytoplankton development may be different.

In geological time scales, changes in phytoplankton have been associated with changes in climate and land cover (Li et al., 2016), tectonic movements (Leroy & Albay, 2010), and geomorphological evolution of lakes, e.g., filling with sediments slowly shifting nutrient availability and light conditions (Brydsten, 2004).

The majority of decadal to centennial-scale changes in lake ecosystems are connected to climate forcing (Adrian et al., 2009) and changes in catchment land use. In contrast, the impacts of these variables are often difficult to unravel (Moss et al., 2011). Interannual to decadal fluctuations of phytoplankton highly correlate with atmospheric circulation patterns such as the North Atlantic Oscillation (NAO) and El Niño-Southern Oscillation (ENSO) that are mainly superimposed on long-term warming trends (Gerten & Adrian, 2002). Besides moderate changes in phytoplankton composition and abundance, environmental forcing may cause lake systems to lose their resilience and exhibit regime shifts, i.e., transitions between alternative and substantially different stable states (Scheffer & van Nes, 2007). Year-to-year changes in phytoplankton are tightly associated with seasonal changes, more precisely with anomalies in seasonality and phenology. For example, different initial conditions of seasonal cycles in temperate lakes – the timing of ice breakup, the height of the spring peak in water levels, duration, and extent of the spring overturn – lead the system to pursue various pathways in their seasonal evolution (Winder & Schindler, 2004). Further, the effect of initial conditions is mainly extended to later parts of the season through match and mismatch processes in the food web (Thackeray et al., 2013).

Direct seasonal changes in light and temperature following the solar cycle and the resulting changes in resource availability mediated by the food chain cause a lake type-specific succession of phytoplankton community repeating to some extend predictably from year to year (Sommer et al., 2012).

However, our interest lies in the poorly understood multiscalar issue related to the response of growth conditions and phytoplankton dynamics to hydrometeorological forcing across time scales (Istvánovics & Honti, 2021).

3 AIMS AND HYPOTHESES OF THE STUDY

In this thesis, we present a synthesis of the relationship between environmental disturbances and phytoplankton in lakes. The thesis is outlined by three published papers each dedicated to a different aspect of the coherent whole (Fig. 1) and has the following aims:

I. To review the possible impacts of storm-induced disturbances on phytoplankton in different lake types. We assume that in case of storms, phytoplankton community dynamics is shaped by changes in physical and chemical structure of the water column (i.e., light, temperature, and nutrients), caused by wind and precipitation and mediated by lake and watershed attributes. The main aim is to build an examinable framework based on published evidence that could be beneficial for future studies related to storm impacts on lake phytoplankton.

II. In the light of the recently discovered robust atmospheric stilling event in the Võrtsjärv area in Estonia in the second half of the 1990s (Woolway et al., 2017), we aim to investigate the impact of this stilling on phytoplankton community in this lake based on the long-term time series (54 years) of hydro-meteorological variables, phytoplankton, nutrients, and optically active substances with setting 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.

III. We aim to motivate limnologists to quantify the impact of hydrometeorological forcing variables on phytoplankton following the variance partitioning among different time scales. We hypothesise that the effect of hydrometeorological forcing variables on phytoplankton at different time scales follows proportionally the variance partitioning of these explanatory variables. Variance partitioning could provide a useful method for disentangling several of the multi-timescale problems.

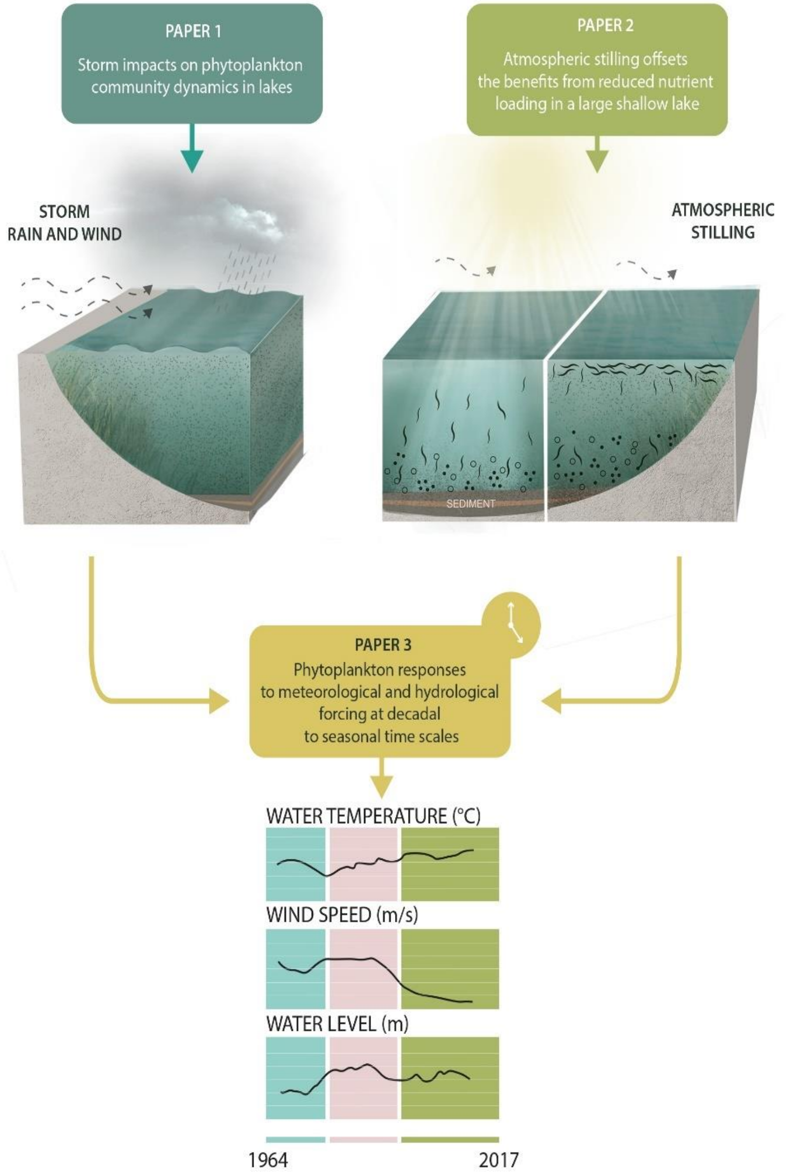

Fig. 1. Graphical outline of thesis

4 MATERIALS AND METHODS

4.1 Review on storm impacts on lake phytoplankton

To assess the effects of storms on phytoplankton dynamics (paper I), a systematic review of the literature was carried out under the leadership by Jason D. Stockwell. Screening the titles and abstracts of the initial 4,346 papers identified through a Web of Science search (1961–2017) using the terms phytoplank* and (storm* or wind* or hurricane* or monsoon* or cyclone* or disturbance*)" yielded 309 papers potentially relevant for "storm effects on phytoplankton" with only 25 of which (including 31 studies) were selected as simultaneously reporting storm effects on physics/chemistry of lentic inland waters with evaluation of phytoplankton responses. The 31 studies included 18 lakes and five reservoirs in 14 countries across Europe (9), East Asia (3), and North America (2). Surface areas ranged from 0.038 to 2,339 km^2 and mean depths ranged from 1.7 to 100 m. Trophic states ranged from oligotrophic to hypereutrophic, with more than half of the water bodies reported as eutrophic or hypereutrophic.

4.2 Study site

For papers II and III, we obtained monthly phytoplankton and daily meteorological data for a total of 54 years (1964–2017) for a large shallow eutrophic lake, Võrtsjärv, located in central Estonia (58°16′N, 26°02′E; II, Fig. 1). Võrtsjärv has a surface area of 270 km^2, mean depth of 2.8 m, and maximum depth of 6

m. The lake is ice-covered for an average of 131 days a year, commonly from end of November to mid-April (Nõges & Nõges, 2012). Interestingly, this number has changed in recent years as permanent ice formation was delayed by approximately two weeks over the years 2007-2018 because of warming (Öğlü, 2021).

The available long-term data for Lake Võrtsjärv (hydrology since 1923, water temperature since 1947, hydrochemistry and biota since the 1960s) make the lake a testable and valuable model area to study the possible phytoplankton responses to meteorological disturbances and global change effects for shallow lakes. Since the late 1970s, cyanobacteria taxa such as *Limnothrix redekei* (Goor) Meffert and *L. planktonica* (Wołosz.) have been the main dominants replacing the earlier *Planktolyngbya limnetica* (Lemm.) J. Komárková-Legnerová. Nowadays, the two species build up 60-90% of the total phytoplankton biomass.

4.3 Data

Phytoplankton abundance and composition, water chemistry, and water transparency (Secchi disk) data collected monthly from four pelagic stations in the lake during the ice-free periods (May-October) over a 54-year period (1964-2017) formed the limnological database used in papers II and III. The 54-year phytoplankton time series has been analysed by two microscopists: Reet Laugaste, until the end of 1977, and her trainee Peeter Nõges afterward.

Daily time-series of wind speed at 10 m height (U) and incident photosynthetically active radiation (PAR_0) were received from the closest meteorological station to the lake (Tõravere, 20 km). We used surface water temperature (SWT) and lake water levels (WL) from the database of the Estonian Institute of Hydrology and Meteorology. The mean PAR within the mixed layer (PAR_{mix}) was calculated based on PAR_0, Secchi depth (SD), and WL using the equation for mixed layer irradiance by Riley (1957). These calculations appear as Eq. 1, Eq. 2, Eq. 3 in paper III.

To evaluate the alteration in the relative proportion of different optically active substances (OAS) in total light attenuation, we assumed that the total attenuation is the sum of attenuations caused by pure water (k_W) and the different OAS (Åberg & Rodhe, 1942) each of which is a product of its concentration and specific attenuation coefficient (C'). For Estonia that belongs to the hemiboreal climatic region, the major OAS in lakes are phytoplankton pigments, TSS total suspended solids (TSS), and colored dissolved organic matter (CDOM) (Eq. 4, II).

CDOM, TSS and total nutrient data were measured following valid standards at the accredited laboratory of Tartu Environmental Research Centre Ltd.

4.4 Statistical methods

To analyse long-term changes in phytoplankton composition, we used Nonmetric Multidimensional Scaling (NMDS) (Ramette, 2007). Specifically, the NMDS was used to compact the information from multiple dimensions into just a few categories. A Bray-Curtis dissimilarity matrix was computed from the community matrix constructed from quantitative biomass values (metaMDS with two-axis; “Vegan” library in R) (II).

We utilized wild binary segmentation (WBS) to detect the change-point in the mean values and variance of phytoplankton and hydrometeorological data using R packages “breakfast” and “WBS” (Baranowski & Fryzlewicz, 2014; Fryzlewicz, 2014). To implement homogeneous, equally distributed data as required by the WBS approach, we used data from Station 1 with a complete set of monthly (May–October) records (II).

The nested random effects statistical model (lmer function of the “lme4” library in R) was applied to explain the hierarchical structure of the time series. We used this method to distinguish which time scales were describing most of the variation within the phytoplankton groups and environmental forcing factors. The error terms contained “residual” variability caused by measurement errors and time scales not accounted for. However, our lack of interest in the mean value of the variables at any time scale led us to use a mixed effect model to calculate the separate variance components (III).

We estimated variance components as underlying the partition-level (e.g., the variance of the time scale) parameters over the other time scales. We made calculations to illustrate the model structure applied for each aggregated phytoplankton and hydrometeorological variable (Eq. 4) in (III).

In addition, to the methods described above, to reveal the influential time scales, we compared the correlations of phytoplankton variables with the original non-transformed and three variants of detrended environmental variables after extracting (i) the seasonal component, (ii) the long-term trend, and (iii) both the seasonal and long-term components. Detrending was done using generalised additive models (GAM) (GAMfunction of the “mgcv” library in R) with regressing the hydrometeorological variables against (i) the day of the year, (ii) the year, and (iii) both the day of the year and year. Comparing the correlation results of the respective detrended variables with phytoplankton highlights whether the correlation is based on the long-term, seasonal, or episodic short scale effect.

Next, based on the daily wind data, we evaluated the daily impact of wind forces calculating shifted correlations between phytoplankton variables and daily average wind with a lag of 0-4 days before phytoplankton sampling (III).

5 RESULTS AND DISCUSSION

5.1 Conceptual model of storm in limnology

We constructed a conceptual model on how storm characteristics combined with lake and watershed properties transform lake conditions (e.g., stratification, nutrient and sediment loading, residence time) determining the living conditions for biota (Fig 2) that has direct implications for ecosystem services provided by the lake.

5.2 Storm effects on phytoplankton dynamic

5.2.1 Effect of wind mixing

The impacts of the same storm will differ between lakes depending on lake and catchment properties and antecedent conditions. Therefore, although the "strength" of a storm is essential, its water column affects such as upwelling, photic zone temperature, mixing depths, and sediment/nutrient resuspension are affected by the interaction with lake bathymetry, area and orientation (i.e., fetch) relative to wind direction. Increasing wind impact on lake surface temperature, light availability for phytoplankton, and internal nutrient loading increases with surface area, however, is mediated by lake depth. Decreased water column stability increases mixing depth (z_{mix}) relative to the euphotic depth (z_{eu}), and thus decrease the effective day length experienced by phytoplankton. Lakes with large surface area (and fetch) can also be affected by stronger sediment resuspension resulting in a reduction in z_{eu}, especially if they are shallow.

Wind-induced mixing and upwelling can also cause internal loading associated with nutrient transport from deeper waters and/or sediments to the euphotic zone. Nevertheless, in shallow lakes, low oxygen can boost internal loading from the bottom sediment (Gerling et al., 2016; Wilhelm & Adrian, 2008). In contrast, in deep lakes, sediment internal loading is usually smaller due to lower nutrient concentrations and lower rates of hypolimnetic oxygen consumption. However, relatively high sediment oxygen demand may occur in deep meso-eutrophic lakes resulting in high phosphorus release rates.

5.2.2 Effect of rainfall

We expect that precipitation influences external loading and affects light availability because of sediment loads. Further, a positive relationship exists between the flushing rate and the watershed area to lake surface area ratio (WA: LSA), which is an indicator of external water, nutrient, and sediment loads showing the extent to which they may impact a lake. In extreme cases, system flushing could potentially prevent additional external loading by flushing nutrients out of the system. Compared to other meteorological phenomena, the influence of precipitation on lake surface temperatures is relatively vaguely understood.

Turbidity also is an important parameter affecting lake surface temperature. Since suspended solids in water absorb and scatter sunlight, near-surface water layers in turbid lakes warm more than in transparent lakes. In this way, erosion flow with storm waters increasing turbidity could also raise water temperature. The sensitivity of a lake to storm impacts is lake type dependent. Shallow and small lakes with surface inflows and outlets generally have short hydraulic residence times of weeks to months and fast flushing rates that makes them sensitive to precipitation while larger and deeper lakes with longer residence times of decades to centuries accumulate the storm runoff and may have longer aftereffects due to extended “memory” of the system.

5.2.3 Antecedent conditions

The antecedent conditions of lakes and their watersheds, such as soil frost and lake ice, soil conditions, thermal stratification, and land use, can further alter the effects of wind and precipitation on in-lake light, nutrients, and temperature conditions (Figure 2d, I). However, how the storm changes the lake's environmental conditions will depend not only on the storm itself but also on many attributes substantial to the lake and its watershed. For example, due to the increased resistance to mixing in stratified lakes, we expect a negative relationship between internal loading to the photic zone and stratification strength before a storm. Consequently, the timing of storms associated with antecedent conditions in lakes and their watersheds plays a crucial role for the impacts of storm-induced mixing and external loading on factors driving phytoplankton communities dynamics. Hence, we propose that phytoplankton diversity at the extreme disturbance (storm) frequency will be related to storm intensity and the lake conditions (stratification) prevailing before the storm.

5.3 Translating a meteorological storm to a "limnological storm"

The following research directions and strategies will enhance our understanding of storm impacts on phytoplankton communities in the future:

- The linkage of lake and watershed attributes and antecedent conditions
- Integration of trait-based and lake models
- Integration of watershed and lake hydrodynamic models
- Sampling frequency, timing, and spatial coverage
- Emerging technologies
- Collaboration as a way forward

Our review presents a framework to methodically check how the large and complex factors and processes involved in translating a meteorological storm to a phytoplankton community can interact.

The application of trait-based models to examine hypotheses about population, community, and ecosystem-level dynamics is challenging because such models perform well in lab experiments but might not show organisms' responses in natural settings. Therefore, our review demonstrates that simulating functional diversity and dynamics with more detailed and mechanistic phytoplankton modules will be needed to integrate multiple trait-based approaches for the next generation of lake models.

Also, direct and indirect pathways by which storms influence lake ecosystems are crucial to evaluate if meteorological storms translate into "limnological storms," which can be applied by coupling watershed and lake models. Coupled watershed and lake models should technically be developed to control the mismatches among model types, including different timescales or different water quality constituents under simulation, and to be able to enhance the accuracy through the model chain (I, III).

The weekly to monthly frequency of data collection in long-term monitoring programs affects our perception of which factors are essential drivers to detect storm effects on phytoplankton dynamics under various timescales and conditions.

Furthermore, our review demonstrates that a sampling range of once every two days is probably the best suitable time scale to investigate the influence of short-term EWEs on phytoplankton dynamics (I, III). Access to new technologies such as remote sensing and autonomous underwater vehicles and their application across systems will enhance our understanding of phytoplankton's spatial and temporal patterns, including storm impacts on plankton communities. In short, a unified collaboration by empiricists, theoreticians, data scientists, modellers, limnologists, and watershed scientists in a global network (e.g., GLEON, NETLAKE, MANTEL, etc.) will be needed to develop and advance a synthetic framework of EWEs, including storm impacts on phytoplankton.

5.4 "Light niche", the meteorological control over phytoplankton in light-limited shallow lakes

Nonmetric Multidimensional Scaling (NMDS) ordination related to phytoplankton community composition in 471 ice-free period samples collected over 54 years from the main monitoring station in Võrtsjärv showed three clusters in the aggregated phytoplankton variables and environmental variables (II, Fig. 3). The NMDS ordination plot of the phytoplankton community composition resulted in two gradients:

1. Aggregated phytoplankton parameters. Despite the biomass of small coccal and colonial forms of green algae and cyanobacteria was negatively associated with NMDS1, the biomass of the dominant phytoplankton (filamentous cyanobacteria and diatoms) scaled positively with it. Moreover, the NMDS axis 2 scores scaled with the motility trait of taxa with flagellates and gas vacuolated cyanobacteria tightly banded at one end of the NMDS axis 1 and benthic diatoms at the other end of this distribution (II, Fig. 3a).
2. The NMDS1 was most negatively linked with bottom shear stress and positively with the light limitation indicator z_{mix}/z_{eu}.

> In the environmental variable zone, psychrophilic benthic and periphytic diatoms in plankton closely corresponded to intense mixing events in spring when the WLs are high following the flood peak. In contrast, the greater biomass of cyanobacteria and flagellates was at the opposite condition with warmer and more turbid (higher k_d) waters in summer when the WLs are generally low. Also, strong polarity in the NMDS2 affected by WL and SWT indicates that this axis mainly characterizes the lake's seasonality (II, Fig. 3b).

The WBS analysis of daily data revealed an abrupt decline in wind speeds since 1996 (atmospheric stilling) (II, Table 1) which caused 43% lower bottom shear stress in the period since 1996 compared to the earlier period of 1966–1995 (II, Table 1). Due to extraordinarily rainy autumn in 1978, the water level (WL) increased sharply, reaching an absolute value (34.99 m above sea level) that exceeded the long-term autumn average for this lake by nearly 1.7 m. In September 1996, the lowest ever WL was reached in the continuous record since 1923.

These two breaking points coincided with the ones that appeared in phytoplankton community composition and, partly, abundance. The lowest ever WL in 1996 was not the breaking point but could function as an additional trigger of change in the phytoplankton community. The first jump between (1977–1978) in NMDS1 and (1978–1979) in NMDS2 matched with a sudden increase in the mean WL (1977– 1979) (II, Figs. 4a–c). The second breaking point in NMDS2 (1996– 1997) was synchronous with the atmospheric stilling (II, Fig. 5(d)). These two jumps in NMDS2 split the 54-year time-series into three periods with different phytoplankton community structure figuring the three clouds in the ordination graph (II, Fig. 3): Period 1 (1964–1977), Period 2 (1978–1996), and Period 3 (1997–2017).

The relative share of the most abundant phytoplankton classes in the total biomass showed a stable trend over the years with a negligible upward trend in cyanobacteria dominance, mainly between Periods 2 and 3 (II, Fig. 6a).

We compared the average biomass changes at species level between Periods 1, 2, and 3 to determine the most prominent "losers" and "winners." The change from Period 1 to Period 2 with a jump in both NMDS scores indicated the shift 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 reflected only in NMDS2 was distinguished by a further decrease of *P. limnetica*, decreasing share of *L. redekei* among the dominants, and an increase of *L. planktonica* biomass (II, Fig. 6b).

The first breaking point between NMDS periods between 1977 and 1979 was linked to an extreme increase in the WL, resulting in deeper mixing. The significant positive correlation between the WL and CDOM throughout CDOM measurements (since 1989) indicates that the higher water in earlier years presumably also carried more CDOM, further worsening the light conditions. Dropped light levels in the mixed layer resulted in replacement of the dominant phytoplankton species with more shade-tolerant ones. The shade-tolerant cyanobacteria species belonging to Oscillatoriales and Nostocales, and the benthic diatoms were the typical group representatives.

These changes in z_{mix}/z_{eu} ratio indicating a deterioration of light conditions in the lake since Period 2, coincided with an upward trend in Chl-a and phytoplankton biomass, primarily due to an increase in *Limnothrix* spp. belonging to Oscillatoriales. Hence, as the dominant species in Võrtsjärv are light-limited, the phytoplankton seems insensitive to changes in nutrient availability. The competitive success of *L. planktonica* could be supported by an increase in water temperature as the species has likely a higher temperature optimum than *L. redekei* and reaches its biomass peak later in the season. Alternatively, it may also be associated with its allelopathic inhibiting effect on other algae, as explained by Tassigny & Lefevre, 1971.

Contrary to expectations, our results demonstrate an upward trend in the concentrations of Chl-a and TSS since 1996, despite a continuous reduction in nutrient concentrations. Surprisingly, we found no decline in optically active substances, which could be associated with wind stilling. Here we present an hypothetical mechanism of the "light niche" created by a declining amount of suspended sediments, which was captured and filled by the light-limited phytoplankton community as explained in the conceptual diagram (Fig. 2). We could identify the replacement of decreasing amounts of suspended sediments by phytoplankton biomass by two analyses:

In the modelled OAS, role of Chl-a in total light attenuation increased while that of TSS decreased in the stilling period. The ratio of phaeopigment to Chl-a, used as an indication for suspended sediments, indicated continuously low values and declined variability after 1996.

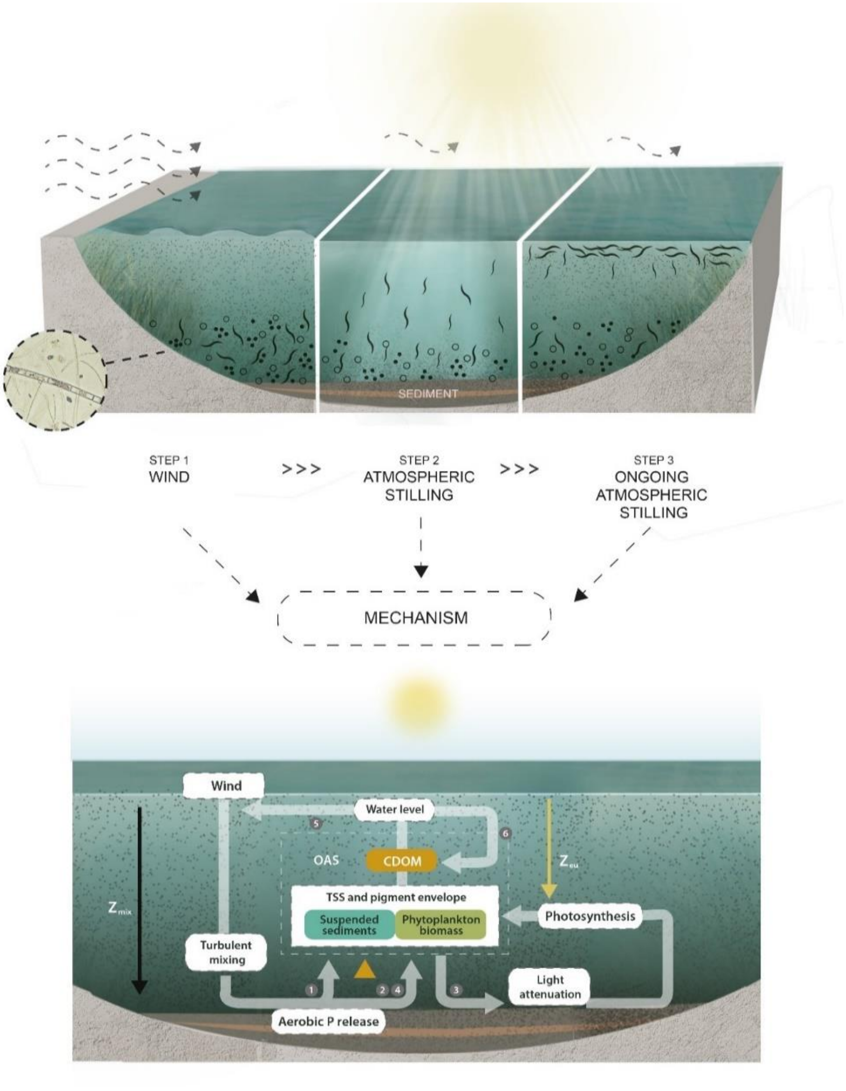

Fig. 2. Schematic outline of the three periods distinguished in Võrtsjärv ecosystem development over the last half century and the plausible mechanism of the changes. See paper II, Fig. 10 for more explanation.

5.5 Variance partitioning – an approach to tackle multiscalarity issues

Variance partitioning in variables among different time scales

Variance partitioning revealed the significance of all four-time scales (decadal, year-to-year, seasonal, and episodic) for both the environmental and phytoplankton variables but considerable differences in their shares between phytoplankton groups (III, Fig. 4a, Table S1). The summary of variance partitioning among time scales in explanatory variables demonstrated the leading role of the WL at the year-to-year scale. Nutrients and Secchi depth shared the second position among major factors acting on an annual scale. Except for wind speed, all hydrometeorological variables had a significant variability (about half or more) related to the seasonal time scale. The residual or error part associated with the most stochastic factors showed a remarkable influence of wind at this timescale. For wind, this component constitutes more than 60%. Cyanobacteria characterised among phytoplankton groups by the highest share of variability in the seasonal component, were strongly controlled by temperature and light. As the dominant phytoplankton group (32-45%), cyanobacteria also controlled the total biomass. Two algal groups – chlorophytes and diatoms – showed significant relationships with the stochastic component of wind, both with the instant wind of the sampling day, and lagged wind 1–4 days before phytoplankton sampling. Diatoms showed an immediate response to wind, showing that stirring up by the turbulent mixing was an important factor for these algae. The biomass of chlorophytes was more dependent on the winds of the day before, showing that their increase was more likely caused by a stimulating effect of nutrients released from the sediments by resuspension. Due to the cyanobacteria dominance in Võrtsjärv, the decadal variance was associated with cyanobacteria and the total biomass of phytoplankton. The inter-annual differences indicated 17-21% of the variance in the total biomass and the cyanobacteria order Nostocales. The minor groups of phytoflagellates – chrysophytes and cryptophytes – explained no variability attributable to decadal periods, cryptophytes also to interannual scale.

5.6 Critical assessment of the statistical methods

Based on long-term (54-year monthly time-series) meteorological and phytoplankton data available from Võrtsjärv, we examined the influence of hydrometeorological forcing of lake phytoplankton community variation at multiple time-scales. We used two approaches:

1. Variance partitioning of phytoplankton and environmental variables with mixed effect linear models with hierarchically nested time scales.

2. Comparative correlation analysis in which we statistically removed the seasonal and long-term interannual trend components from the descriptive hydrometeorological data.

We found that both implemented statistical approaches successfully captured coherent results for tracking our intuitive understanding of the dynamic behaviour of the different driving factors:

1. Both methods corroborated the putative role of the stochastic component in the wind and the seasonal component in the water level and mixed layer PAR.
2. Our results confirmed the hypothesis that variance partitioning among the time scales is a credible, practical, and straightforward technique for untangling the multi-scale time problem with easily interpretable quantitative results.

The correlation analysis approach has proven effective in identifying the dynamic behaviour of the different variables in some validated cases. In contrast, we emphasize that tracking many individuals pairwise combinations may cause inflation of the type I error related to multiple comparisons. Therefore, we demonstrated that the significant positive or the negative relationship could be considered possible hypotheses for future study. Also, if the hydrometeorological forcing on phytoplankton poorly supports the proportionality of the variance partitioned within these factors, false correlations, incoherence, and error may appear.

The analyses demonstrated the robustness of the variance partitioning results in limiting false results. This approach correctly identified instances in which the variance partitioning in the environmental driving factors matched the time scales of the impacted phytoplankton groups. However, the analyses also indicated contradictions that correlation analysis results did not fully validate the outcomes of variance partitioning. We cautiously criticize the spurious character of some correlations. For example, variance partitioning indicated that only a negligible part of the variability in WL was based on stochastic changes. In contrast, the correlations of phytoplankton with the stochastic component of WL remained significant. However, the negligible attribution of stochastic changes in WL is entirely understandable due to a robust autocorrelated character of this variable. However, the significant correlations of phytoplankton with the stochastic component are not easy to interpret.

Furthermore, our analysis revealed that detrending of the hydrometeorological variables could either strengthen or weaken the correlations with phytoplankton. To be conservative with the possible chaotic variability of different environmental driving factors in diverse temporal components, which raises red flags, meaning that we should apply detrending carefully to keep the valuable parts of data before scraping the results. However, we suggest that screening variables using variance partitioning are a delightful option for future studies.

6 CONCLUSIONS

This thesis presents a framework to highlight that, lakes can be strongly affected by extreme events like storms and long calm periods, whereas the sensitivity to and recovery from such events is lake type specific and may extend over different spatial scales. Therefore, the manifestation of such events in lake states is particularly time-scale dependent and not a simple consideration or single function of the event strength at a specific point in time and space. The main focus on air temperature change in climate impact studies has distracted attention from the possible effects of different elements of climate change like storms or wind stilling. This thesis contributes to understanding of the influences of storms and atmospheric stilling as other important factors of climate change affecting lakes.

In paper I we had to recognise that the understanding of the effects of storms, a combination of strong wind and torrential rainfalls, on lakes, and specifically on lake phytoplankton, is modest. The issues require to be explored further by adding a watershed-scale approach, examining the relationships among storm, lake, and watershed characteristics to understand the mechanisms of multiple controlling factors affecting phytoplankton dynamics at different time scales (Fig 1). Hence, enhancing the knowledge includes considering antecedent conditions, integration of models, improving sampling frequency and spatial coverage and applying new technologies in monitoring. So far, we do not fully understand the mechanisms of multiple driving factors affecting phytoplankton dynamics at different time scales. Our review indicates the need to integrate aquatic ecosystem conservation and restoration with climate change context. Therefore, we will need to improve our knowledge of the extent to which storms diminish ecological resilience and what are the implications for ecosystem services provided by lakes.

In paper II we distinguished three periods based on phytoplankton community composition in Võrtsjärv, a large shallow eutrophic lake in Estonia, over the 54-year time period. The time-series was split by a sudden WL increase between 1977 and 1979, and wind stilling since 1996. These environmental variabilities increased the competitive advantage of *K*-selected phytoplankton dominated by shade-tolerant thin filamentous cyanobacteria from the genus *Limnothrix*. Our results illustrate that, in periods of unstable environments with increased wind speed and low WL, the successful species were *r*-strategists of small body size and fast-growing rates represented in Võrtsjärv by Chlorococcales, Chroococcales, and Desmidiales. In opposite conditions, the *K*-strategists took advantage of high-water periods related to more stable conditions with less sediment disturbance and lower average light levels in the deeper mixed water column. This corroborated our hypothesis that less frequent episodes of aerobic P release affected by lower wind speeds causing the lower bottom shear stress could suppress *r*-strategists phytoplankton species (II, hypothesis 1).

We hypothesized that the reductions in wind speed, causing changes in water turbulence, would also potentially influence algal groups of different motilities. Therefore, we expected to see fewer meroplanktonic species mechanically dragged into the planktonic compartment but more flagellates that would increase within thermal stratification episodes in summer. Although benthic diatoms were more dominant in the windier Period 2, we found only a nonsignificant correlation between them and the 3-day average shear stress (Shear3D). However, the significant negative correlation of flagellated algae with Shear3D (II, Table 2) revealed the direct consequences of wind impacts on phytoplankton community composition. While turbulence enables passive movement of cells within the water column, motility of cells becomes an advantage in stagnant waters enabling movement within the critical resource gradients (II, hypothesis 2 & 3).

Despite the expected increase in water transparency resulting from the 47% drop in bottom shear stress, we observed no improvement throughout the stilling period. This is mainly because the compensatory growth of low light adapted phytoplankton captured this potential “light niche”. We introduced a theoretical underpinning named “light niche” to explain why we observed empirical evidence of algal biomass growth despite the history of decreasing nutrient concentrations. Besides, why we indicated slightly high-water turbidity despite a downward trend in wind speed (Fig. 2) (II, hypothesis 4).

As our paper II underscored the importance of considering the effect of different timescales while studying relationships between timeseries, we dedicated paper III to in-depth analysis of the impact of hydrometeorological forcing on phytoplankton dynamics at multiple time-scales from days to decades. We used the same long-term database of monthly phytoplankton time series from Võrtsjärv combined with daily hydrometeorological variables. To address the multiscalarity issue, we used two approaches: (1) variance partitioning of phytoplankton and environmental variables and (2) comparative correlation analysis in which we statistically removed the seasonal and long-term interannual trend components from the descriptive hydrometeorological data. Variance partitioning revealed the inherently diverse nature of the environmental variables. Both analyses distinguished three phytoplankton groups differing by their life strategy and stochastic component of their biomass dynamic: (1) the dominant slow-growing filamentous cyanobacteria (*K*-strategists) determining the biomass dynamics of cyanobacteria and the total biomass were characterised by the lowest stochastic and most extensive seasonal and decadal component of variability; (2) chlorophytes and diatoms with an intermediate stochastic variability and (3) two groups of phytoflagellates—chrysophytes and cryptophytes characterised by 80% of stochastic variability. A considerable proportion of the two latter groups was represented by opportunistic *r*-strategists. We introduced variance partitioning as a straightforward method to tackle the temporal cross-scale problem, which could have profound implications on understanding biogeochemical cycling. As the frequency of EWEs is likely to increase with deepening climate crisis, all possible contributions to an out warrant thorough consideration. The role of risk and uncertainty associated with (i) the ecological context in mediating climate crisis impacts, (ii) the substantial heterogeneity in weather conditions globally, and (iii) possible interactions of multiple governing variables driving plankton dynamics at different time scales challenge our ability to fully orient in the impacts of EWEs on water quality, phytoplankton, and ecosystem processes.

However, studying the multiple time-scale problem in plankton ecology is critical for knowledge-based water management.

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SUMMARY IN ESTONIAN

Teadmiste areng järvede fütoplantonit kontrollivate tegurite vallas

Elustiku koosluste struktuuri, mitmekesisust ja dünaamikat kujundavate tegurite väljaselgitamine ja nende konkreetse mõju uurimine on ökoloogiliste uuringute keskseks sisuks (Thomas et al., 2018). Alates Hutchinsoni tööst “plantoni paradoksi” kohta (1961), mis selgitas, kuidas on võimalik paljude liikide kooseksisteerimine piiratud arvu limiteerivate ressursside tingimustes, Tilmani (1977; 1982) teoreetilistest töödest ressursikonkurentsi kohta, Connelli (1979) vahepealse häire rakendamiset plaktoni suktsessiooniteoorias (Reynolds, 1973) ja mõnedest põhjapanevatest toiduahela uuringutest (nt Leibold, 1966), ei ole fütoplanktoni arengut selgitavates teooriates võrreldava suurusega läbimurdeid viimasel ajal toimunud. Paljud autorid on sunnitud nentima, et fütoplanktoni arengut kujundavas mõjuväljas on endiselt palju teadmatut, mis tuleneb mittelineaarsetest seostest atmosfääri, hüdrosfääri ja biosfääri vahel (Francis et al., 1998), alanevate ja ülenevate mõjuahelate tasakaaluolekust toiduahelas (Schurin et al., 2012), tegurite koosmõjust (Nõges et al., 2016), aga ka pikaajaliste kvaliteetsete planktoni andmete puudusest, et aastakümnetesse ulatuvate muutuste mõjusid uurida. Jätkuvate planktoniökoloogiliste uuringute käigus kogunev tõendusbaas sillutab aga loodetavasti teed uuteks läbimurreteks.

Kliimamuutusega seoses on sagenenud tormid (Hegerl & Min, 2013; Lehmann et al., 2015), kuid paradoksaalselt on täheldatud ka paljudes maailma piirkondades tuulte nõrgenemist (Woolway et al., 2019). Mõlemal teguril on kaugeleulatuvad tagajärjed järvede veesamba stabiilsusesse, mis mõjutab vahetult fütoplanktonile kõige olulisemate ressursside – toitainete ja valguse – kättesaadavust. Tormid mõjutavad järvi lõhkudes veesamba termilist kihistust, kandes planktonit järve hämaratesse süvakihtidesse ja segades üles põhjasetteid, mille käigus vabanevad sinna ladestunud toitained. Tormidega kaasnevad vihmavalingud võivad põhjustada pinnase erosiooni ja suurendada valglalt lähtuvat toitainekoormust. Kestvatel tuulevaikuse perioodidel on vastupidine toime: tugev termiline kihistumine võib isoleerida järve seguneva pinnakihi sügavamatest, mille tagajärjel vaesub pinnakiht toitainetest, põhjakihis võib aga kujuneda hapnikupuudus. Mõlema teguri puhul on oluline teada, kui kestev nende poolt põhjustatud mõju on ja kuidas see sõltub teguri intensiivsusest, aga samuti järve ja valgla omadustest ning varasemate häiringute ajaloost.

Fütoplanktoni kooslust mõjutavad üheaegselt nii pikaajalised nihked mõjutegurites, aastatevahelised erinevused, suhteliselt regulaarne sesoonne muutlikkus ja juhuslikku laadi lühiajalised häiringud. Nende erinevas ajaskaalas toimivate mõjutuste eristamine planktoni kumulatiivses reaktsioonis on üks põhiküsimusi, mis seni takistab fütoplanktoni dünaamika mõistmist. Võrtsjärve kohta enam kui 50 aasta jooksul kogunenud igakuine fütoplanktoni aegrida koos igapäevaste hüdroloogia- ja ilmastikuandmetega pakub unikaalset võimalust mitmete planktoni ökoloogiat puudutavate küsimuste lahendamiseks.

Uuringu eesmärgid

Püstitasime käesolevas töös järgmised eesmärgid:

1. Anda ülevaade tormide mõjust järvede fütoplanktonile ja selgitada tegurid, mis seda mõju muundavad ja vahendavad. Üritasime kirjanduse põhjal luua analüüsitavat tõendusbaasi, mis koondaks antud teemal olemasolevad teadmised ja mis oleks suunanäitajaks edaspidistes uuringutes.

2. Hiljutise avastuse valguses, et Võrtsjärve piirkonnas on tuulte keskmine kiirus oluliselt vähenenud alates 1990. aastate teisest poolest (Woolway et al., 2017), seadsime eesmärgi uurida selle sündmuse mõju järve füüsikalistele, keemilistele ja fütoplanktoni näitajatele. Püstitasime järgmised hüpoteesid:

H1: Nõrgemate tuulte mõjul nõrgeneb nihkepinge järve põhjasetetele, mille tagajärjel harvenevad fosfori aeroobse vanemise episoodid ja surutakse alla neist toituvate kiirekasvuliste oportunistlike vetikaliikde (*r*-strateegide) areng.

H2: Nõrgema nihkepinge tõttu sette pinnal väheneb meroplanktiliste (bentiliste ja perifüütiliste) liikide esinemine planktonis, kuna nõrgemas turbulentsis on neil vähem võimalust substraadilt lahtirebitud saada.

H3: Kestvamad termilise kihistumise perioodid soodustavad liikumisvõimeliste (viburitega) liikide arengut, kuna need saavad stagneerunud veesambas migreerudes valida endale sobivaid valgus- ja toitainetingimusi; samuti on soodustatud pindmisi veeõitsenguid põhjustavad sinivetikaliigid, kes vajavad pinnakihti kogunemiseks tuulevaikust.

H4: Harvenevad settehäiringud parandavad tingimusi aeglasekasvulistele valguslimiteeritud fütoplanktoni liikidele (*K*-strateegidele), kuna vette satub vähem põhjasetteid. Paranevad valgusolud võimaldavad neil oma biomassi suurendada. Tulemuseks on, et setteosakeste osakaal üldises valguse nõrgenemises väheneb, fütoplanktoni osakaal aga suureneb, mistõttu vee läbipaistvus ei pruugi lõpptulemusena paraneda.

3. Selgitada muutlikkuse jaotamise (ingl. k. *variance partitioning*) statistiliste meetodite sobivust erinevates ajaskaalades toimuvate muutuste eristamiseks. Need meetodid aitavad sügavamalt mõista ökoloogiliste seoste olemust ja annavad vihjeid põhjuslike seoste kohta.

H5: Hüdrometeoroloogilised tegurid mõjutavad fütoplanktonit erinevates ajaskaalades proportsionaalselt nende muutlikkuse jaotusega erinevate ajaskaalade vahel. Näiteks, kui päikesekiirguse suurim muutlikkus jääb ööpäevasesse ja sesoonsesse skaalasse, ei ole erilist mõtet otsida päikesekiirguses põhjusi fütoplanktoni aastatevaheliste muutuste või pikaajaliste trendide selgitamiseks.

Materjal ja metoodika

Lähtematerjal ülevaateartikli (**I**) koostamiseks tormide mõjust fütoplanktonile koosnes 4346 *Web of Science* pealkirjade kaudu valitud artiklist aastatest 1961–2017. Nende sõelumine pealkirjade ja abstraktide põhjal kasutades otsisõnu phytoplank* ja (storm* või wind* või hurricane* või monsoon* või cyclone* või disturbance*) tõi esile 309 antud teema kohta potentsiaalselt olulist artiklit, millest lõpuks jäi sõelale vaid 25 (mis sisaldasid 31 uuringut), kus üheaegselt leidus andmeid tormide mõju kohta järvede füüsikalistele ja keemilistele näitajatele ning oli ka kirjeldatud fütoplanktoni reaktsiooni neile muutustele. Need 31 uuringut hõlmasid 18 järve ja 5 veehoidlat 14 riigis Euroopas (9), Ida-Aasias (3) ja Põhja-Ameerikas (2).

Artiklite **II** ja **III** puhul kasutati Võrtsjärve kohta 54 aasta jooksul igakuiselt kogutud andmeid vee läbipaistvuse, temperatuuri, keemiliste näitajate ja fütoplanktoni kohta (töös leidsid kasutamist küll ainult jäävaba perioodi andmed maist oktoobrini).

Keskkonnaparameetritena kasutati lisaks igapäevaseid Rannu-Jõesuus mõõdetud veetaseme andmeid ja Tõraveres mõõdetud ilmastikuandmeid.

Tuule kiiruse ja suuna ning vee sügavuse põhjal arvutati setetele mõjuv nihkepinge. Veepinnale langeva kiirguse, vee läbipaistvuse ja sügavuse põhjal arvutati veesamba keskmine valgustatus. Valguse nõrgenemine veesambas jagati erinevate optiliselt aktiivsete ainete (üldheljum, klorofüll ja huumusained) vahel vastavalt nende ainete kontsentratsioonidele ja erineeldumisele.

Fütoplanktonikoosluses toimunud muutuste periodiseerimiseks (**II**) kasutasime Bray-Curtis erinevuste maatriksi mitmemõõtmelist analüüsi (Nonmetric Multidimensional Scaling, NMDS). Murdepunktide leidmiseks aegridades kasutasime Wild Binary Segmentation (WBS) meetodit (Baranowski & Fryzlewicz, 2014; Fryzlewicz, 2014).

Parameetrite muutlikkuse jaotumise uurimiseks erinevate ajaskaalade vahel (**III**) kasutasime hierarhilist (nested) mudelit, mille jääkliige iseloomustas mõõtmisvigadest ja lühimates ajaskaalades toimunud juhuslikest muutustest tingitud muutlikkust. Lisaks kasutasime korrelatsioonide võrdlust, milles fütoplanktoni andmeid korreleeriti keskkonnaandmete nelja versiooniga: (i) originaalandmetega, (ii) detrenditud andmetega, (iii) andmetega pärast sesoonse komponendi kõrvaldamist ja (iv) pärast trendi ja sesoonsuse kõrvaldamist. Nimetatud muutlikkuse osad kõrvaldati üldistatud lisandmudeli (Generalised Additive Models, GAM) abil.

Tulemuste kokkuvõte

Kirjanduse ülevaate tulemusena loodi kontseptuaalne mudel (joon. 2), mis näitab, kuidas tormi omadused koosmõjus järve ja valgla omadustega määravad tormi mõju ulatuse ja iseloomu järve hüdroloogilisele, keemilisele ja optilisele seisundile ja selle kaudu järve elustikule ning ökosüsteemi poolt pakutavatele teenustele. Loodud tõendusbaas koondab tormi mõjude kohta tehtud tähelepanekud parasvöötme eritüübilistes järvedes ja on aluseks uuringute jätkamisel tulevikus.

Võrtsjärvest 54 aasta jooksul jäävabal ajal kogutud fütoplanktoniproovide andmete ordineerimine NMDS abil eristas kolm koosluse koosseisu poolest erinevat ajaperioodi. NMDS telg 1 iseloomustas fütoplanktoni elustrateegiate gradienti seostudes negatiivselt väikeste kokoidsete rohe- ja sinivetikatega (*r*-strateegid), positiivselt aga domineerivate aeglasekasvuliste ja varjutaluvate niitjate sinivetikatega (*K*-strateegid). Viimased olid soodustatud ja *r*-strateegid alla surutud kõrgema veetasme perioodidel, mil sette häiringud harvenesid toetades meie **hüpoteesi H1**.

Oletasime, et tuulte nõrgenemine põhjustab muutusi erineva liikuvusega vetikaliikide vahekorras, kuna raskeid meroplanktilisi liike haaratakse vähem sette pinnalt ja taimedelt kaasa veesambasse, viburitega liigid aga saavad seisvas vees eelise. Ehkki meroplanktonisse kuuluvaid bentilisi ränivetikaid oli kõrgeveeperioodil vähem, jäi nende biomassi korrelatsioon sette pinnal toimiva nihkepingega siiski statistiliset mitteoluliseks, mistõttu **hüpotees H2** ei saanud veenvat tõestust, kuid ei lükatud ka ümber. Viburitega vetikate biomassi ja proovivõtule eelneva kolme päeva keskmise nihkepinge vahel oli aga usaldusväärne negatiivne korrelatsioon, mis kinnitas meie **hüpoteesi H3** näidates, et stagnatsiooni tingimustes on aktiivne liikumisvõime kasulik, kuna võimaldab vetikatel muuta oma asendit veesambas kriitiliste ressursside (valgus ja toitained) gradientides.

Vaatamata järve põhjale mõjuva nihkepinge 47 % vähenemisele alates 1996. aastast tuulte nõrgenemise tõttu, ei paranenud vee läbipaistvus nagu võinuks eeldada nõrgema setete segamise tingimustes. Vähenenud setteosakeste hulga kompenseeris valguse poolt limiteeritud fütoplanktoni täiendav kasv. Sellest muutusest andis tunnistust nii setteid inditseerivate feopigmentide hulga vähenemine kui ka vetikatele omase klorofüll-*a* hulga suurenemine, mis mõlemad toetasid meie **hüpoteesis H4** sõnastatud nn “valgusniši” teooriat (joon. 3).

Kuna meie **artikli II** tulemused näitasid erinevate ajaskaalade arvestamise tähtsust aegridade vaheliste seoste uurimisel, pühendasime **artikli III** keskkonna- ja vetikanäitajate variatsiooni jaotuse uurimisele erinevate ajaskaalade vahel päevadest aastakümneteni kasutades sama pikaajalist Võrtsjärve andmebaasi nagu eelmise uuringu puhul. Muutlikkuse jaotumine tõi esile olemuslikud erinevused keskkonnategurite vahel. Kui näiteks temperatuuri ja kiirguse näitajatel oli suurim proportsioon sesoonsel muutlikkusel, siis tuule kiiruse muutlikkuse raskuskeskmed olid päevastel ja aastakümneid iseloomustavatel komponentidel. Fütoplanktonis eristus muutlikkuse jaotuse alusel kolm rühma: (1) domineerivad aeglasekasvulised sinivetikad (*K*-strateegid), kelle puhul oli vealiikmesse koondunud lühiajalise ja juhusliku muutlikkuse komponent väikseim; (2) rohe- ja ränivetikad mõõduka juhusliku variatsiooni komponendiga ja (3) kaks rühma flagellaate – kold- ja neelvetikad, kelle puhul juhusliku ja lühiajalise varieeruvuse komponent ulatus 80%-ni. Arvestatava osa kahe viimase rühma vetikatest moodustavad oportunistlikud *r*-strateegid. Kui esimese rühma vetikaid mõjutas eelkõige tugevalt autokorreleeritud veetase, siis r-strateegide puhul ilmnesid seosed kiirelt muutuvate näitajatega nagu tuul. See kinnitas meie **hüpoteesi H5**, et hüdrometeoroloogilised tegurid mõjutavad fütoplanktonit erinevates ajaskaalades proportsionaalselt nende muutlikkuse jaotusega erinevate ajaskaalade vahel.

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MANTEL virtual symposium

Outreach_ MANTEL Pieces

👤 Profile

- I have been involved in a double PhD. program (about hydro meteorological and climatic control over lake phytoplankton: the importance of time scales) in the EU2020 MANTEL (https://www.mantel-itn.org/), a Marie Curie Action EJD ITN, started in Oct 2017.
- **MANTEL** (Management of Climatic Extreme Events in Lakes & Reservoirs for the Protection of Ecosystem Services) brings together eight beneficiaries, supported by ten partners and five awarding universities. This consortium has been training a cohort of 12 Early-Stage Researchers (ESR) to investigate the effects on water quality of the climatic extreme events, while at the same time giving training in state-of-the-art technology data analysis, modelling, and linking to the water management sector.
- Experienced in remote sensing and GIS Techniques, satellite image processing, big data analytics, numerical modelling.

💼 Technical skills

- Fluent in R, MATLAB, and experienced in IDL and FORTRAN
- Data analysis
- Statistics
- Numerical modelling
- Modelling
- Remote sensing and GIS techniques:

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Publications

- **Janatian, N.**, Sadeghi, M., Sanaeinejad, S.H., Bakhshian, E., Farid, A., Hasheminia, S.M. and Ghazanfari, S., 2017. A statistical framework for estimating air temperature using MODIS land surface temperature data. ***International Journal of Climatology,*** *37*(3), pp.1181-1194.
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