



Eesti Maaülikool
Estonian University of Life Sciences

**IMPACT OF CLIMATE CHANGE AND OTHER
ECOLOGICAL FACTORS ON SELECTED FISH
POPULATIONS AND FISHERY IN ESTONIAN LARGE
LAKES**

**KLIIMAMUUTUSTE JA TEISTE ÖKOLOOGILISTE
TEGURITE MÕJU VALITUD KALALIIKIDE
POPULATSIOONIDELE JA KALAPÜÜGILE EESTI
SUURJÄRVEDES**

BURAK ÖĞLÜ

A Thesis
for applying for the degree of Doctor of Philosophy
in Applied Biology

Väitekirj
filosoofiadoktori kraadi taotlemiseks
rakendusbioloogia erialal

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Opponent: **Prof. Anna Kuparinen, PhD**
University of Jyväskylä, Finland

Pre-opponent: **Prof. Kalle Olli, PhD**
Estonian University of Life Sciences, Estonia

Supervisors: **Prof. Tanel Kaart, PhD; Külli Kangur, PhD;**
Fabien Cremona, PhD
Estonian University of Life Sciences, Estonia

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Estonian University of Life Sciences, Kreutzwaldi 5, Tartu and web-based on May 28, 2021, at 10:15.

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LIST OF ORIGINAL PUBLICATIONS

The present thesis is based on the following articles, which are referred to by their Roman numerals in the text. The articles are reproduced with the kind permission of the publishers.

- I. Öglü, Burak; Möls, Tõnu; Kaart, Tanel; Cremona, Fabien; Kangur, Külli (2020). Parameterization of surface water temperature and long-term trends in Europe's fourth largest lake shows recent and rapid warming in winter. *Limnologica* .10.1016/j.limno.2020.125777.
- II. Öglü, Burak; Bhele, Upendra; Järvalt, Ain; Tuvikene, Lea; Timm, Henn; Seller, Siim; Haberman, Juta; Agasild, Helen; Nõges, Peeter; Silm, Maidu; Bernotas, Priit; Nõges, Tiina; Cremona, Fabien (2020). Is fish biomass controlled by abiotic or biotic factors? Results of long-term monitoring in a large eutrophic lake. *Journal of Great Lakes Research*, 46(4), 881–890. 10.1016/j.jglr.2019.08.004.
- III. Bernotas, Priit; Öglü, Burak; Nõges, Peeter (2020). How do environmental factors affect the yield of European eel (*Anguilla anguilla*) in a restocked population? *Fisheries Research* 230 (2020): 105649. 10.1016/j.fishres.2020.105649

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ABBREVIATIONS

AIC:	Akaike Information Criterion
AICc:	small-sample equivalent of Akaike Information Criterion
BMI:	benthic macroinvertebrate biomass
COI:	Co-inertia analyses
DO:	dissolved oxygen
GLM:	Generalised Linear Model
GLS:	Generalised Least Squares
HCO_3^- :	carbonate alkalinity
LSWT:	lake surface water temperature
NAO:	North Atlantic Oscillation
NO_3^- :	nitrate
O_2 :	oxygen
pH:	acid-alkaline balance
PO_4^- :	phosphate
r:	Spearman correlation coefficient
R ² :	coefficient of determination
RF:	Random Forest
RV:	coefficient of multivariate analysis
SmWT:	smoothed water temperature
T:	temperature (°C)
TFB:	total fish biomass
TL:	total length
TN:	total nitrogen
TP:	total phosphorus
VIF:	Variance Inflation Factor
WL:	water level
WPUE:	weight per unit effort
WT:	water temperature (°C)
YOY:	young-of-the-year

1. INTRODUCTION

Earth's surface freshwaters carry great importance for being heritage of global biodiversity (Moss, 2000). They are hosting ~ 10% of all known species, one third of vertebrate species and 40% of global fish species (Lundberg et al., 2000; Strayer and Dudgeon, 2010), despite covering less than 1% of the earth surface (Strayer and Dudgeon, 2010). However, anthropogenic pressure and climate change have become the most consequential threats to freshwater ecosystems, especially lakes, in the last decades (Cheng et al., 2010; Woolway et al., 2020). Lakes are one of the most vulnerable systems that are under the major impact of climate change because most of lakes are warming up faster than oceans or atmosphere (Kintisch, 2015; Witze, 2015; Woolway et al., 2020). Hence, lakes can serve as monitoring sites to understand the changes in climate and provide indications of their effect on the ecosystem structure in advance (Adrian et al., 2009; Lynch et al., 2016b).

Lakes respond rapidly to climate change and the most common physical consequences that occur in lakes are a decrease in ice cover duration and warming of surface waters (O'Reilly et al., 2015; Sharma et al., 2019; Woolway et al., 2020). Studies show that the response of lakes to climate change can differ depending on latitude, climate zone, and lake types (Adrian et al., 2009; O'Reilly et al., 2015). Direct external driving factors are yearly and seasonal air temperature, snowfall and evaporation all depending on climate region (Adrian et al., 2009). Lake response to climate change can be manifested as changes in the water level, temperature, stratification, ice phenology, transparency, water chemistry (oxygen, conductivity, pH), and biotic community structure (algal blooms and species composition, invasive species) (Adrian et al., 2009; Bachmann et al., 2020). All those parameters can interact with each other, including also mixing regimes and evaporation rates (Woolway et al., 2020). Winter air temperature changes are among the most important climate factors in boreal lakes that might affect habitat status, productivity, fish production, and water quality (Adrian et al., 2009). Climate change responses of shallow lakes can show dissimilarity compared to deeper lakes (Wetzel, 1990; Winslow et al., 2015). Water column temperature in shallow lakes can reflect the rapid changes in air temperature. Lack of stratification and high surface to volume ratio makes shallow lakes one of the most affected ecosystems by external

factors like climate change (Jeppesen et al., 2009; Moss et al., 2009; Nöges and Nöges, 2014). Furthermore, long term warming can enhance drought and cause negative impact on water levels (Beklioglu et al., 2007; Vincent, 2009).

Ice cover in northern lakes, due to its role in lake stratification and heat storage, has a great importance for the thermal condition of biota (Leppäranta, 2010; Leppäranta et al., 2019; Mishra et al., 2011). Besides, ice phenology and winter temperature are important parameters to evaluate climate impact at northern latitudes. Global climate models project that climate change will have a strong impact on lake ice phenology at northern latitudes in the 21st century (Brown and Duguay, 2010). Loss of ice, winter warming, and a decrease in ice cover period are recorded in different regions of the Northern Hemisphere in recent years (Elo et al., 1998; Filazzola et al., 2020; Karetnikov et al., 2017; Livingstone and Adrian, 2009; Mishra et al., 2011; Naumenko et al., 2008; Sharma et al., 2019). Reduced lake ice cover and risen lake temperature might accelerate evaporation and cause modifications in lake mixing regimes (Woolway et al., 2020). Thus, resulting from unbalance between precipitation or inflow and high evaporation rates, the lake water level may decrease that would impact water quantity and quality, food provisioning, recreational opportunities, and transportation (Woolway et al., 2020).

As a widespread phenomenon and environmental problem (Carpenter, 2005), eutrophication resulting from excess nutrient loading is considered as one of the most important pollution types in lakes (Assessment, 2005; Fink et al., 2018). Eutrophication is also gaining momentum in rate under the negative influence of global warming (Jeppesen et al., 2010b; Meerhoff et al., 2007). Besides external nutrient loading, resuspension of sediment and exchange at the sediment-water interface may increase the concentration of nutrients, especially phosphorus, in shallow lakes (Søndergaard et al., 1992). Also, increased evaporation due to warming can elevate nutrient concentrations in shallow lakes (Landkildehus et al., 2014; Özen et al., 2010). Concentrations of phosphorus (P) and nitrogen (N) and changes in the N/P ratio are among the strongest factors behind the excessive growth of algae (Lv et al., 2011). The synergistic effect of rising nutrient concentration together with an increase in water temperature can accelerate eutrophication and cause the growth of certain algae which may affect the lake ecosystem, including biodiversity (Cai et al., 2012; Chislock et al., 2013; Liu et al., 2011). Primary producers

provide food for zooplankton, however nuisance algae like cyanobacteria and filamentous algae can negatively impact the ecological status of lakes by degrading water quality, causing hypoxia/anoxia and producing cyanotoxins (Brooks et al., 2016; Cremona et al., 2018b; Havens, 2008). Indirect impact of climate change can occur in trophic dynamics and food web interactions via rise in proportion of cyanobacteria among the phytoplankton. This can impact zooplankton composition and thus reduce the piscivorous fish size and abundance through a bottom-up mechanism in the lake (Cremona et al., 2014; Daufresne et al., 2009; Jeppesen et al., 2012).

Lake Võrtsjärv and Lake Peipsi are two large shallow lakes in Estonia interconnected with the Emajõgi River. Both lakes are located in the hemiboreal zone and are the two largest lakes in the Baltic countries. According to nutrient levels (TP: $54 \mu\text{g L}^{-1}$, TN: $748 \mu\text{g L}^{-1}$ in Peipsi and TP: $48 \mu\text{g L}^{-1}$, TN: $910 \mu\text{g L}^{-1}$ in Võrtsjärv), both lakes are considered eutrophic (Cremona et al. 2018b; Kangur et al., 2020). In the Estonian part of the Lake Peipsi catchment, the external nutrient loading, especially from the Emajõgi, was largely reduced by improving wastewater purification systems (Blank et al., 2017). Although external nutrient loading to Lake Peipsi has reduced since the 1990s (Fink et al., 2020), cyanobacterial blooms, anoxia, and fish kills are still recurrent in the lake (Kangur et al., 2020; Kangur et al., 2013). Similarly, in spite of the decreasing nutrient loading to Lake Võrtsjärv since the 1990s, phytoplankton (especially cyanobacteria) biomass has continued to increase (Cremona et al., 2020; Nõges et al., 2010; Nõges et al., 2020).

Fish and fisheries are important for the society by their economic value, the cultural and recreational services they provide, human health/well-being that the fish products support, and their critical role in ecosystem functioning (Lynch et al., 2016a). Studies indicate that marine and inland water fish populations are declining, composition is changing, landings are decreasing all over the globe due to many different reasons such as overfishing, climate change, pollution, and diseases (Allan et al., 2005; Cowx, 2015; Kao et al., 2020; Ngor et al., 2018; Pauly et al., 1998; Tammiksaar and Kangur, 2020). Fish can be affected through biotic interactions, changes in oxygen concentration and other changes in their habitat induced by climate change (Jeppesen et al., 2010a). Most direct responses of fish (e.g. fish kill, migration) to extreme climate events depend on their temperature and hypoxia tolerance (Jeppesen

et al., 2010a; Kangur et al., 2016). Fish survival and growth rates largely depend on temperature (Magnuson et al., 1990), whereas the capacity to adapt to thermal changes differs for cold-, cool-, and warm-water fish species (Lehtonen, 1996). Additionally, the multiple age classes within fish populations respond to temperature in different ways over different timescales depending on their adaptation (Jonassen et al., 1999; Pepin, 1991; Van Dorst et al., 2019). The response of the fish populations to temperature can also influence the entire food web via biotic interaction if the lakes are controlled by the top-down cascading mechanism (Carpenter et al., 1985). The structure of fish communities and populations is also depending on biotic and abiotic interactions in lakes that are under the influence of climate change (De Bernardi, 1981). Abiotic factors comprise physical and chemical components such as oxygen concentration, pH, alkalinity, nutrients, temperature, water level, light, turbidity, and catchment properties, while biotic factors cover food availability, diseases, prey-predator relations, competition and other interspecific relations (Fig. 1) (Gebrekiros, 2016; Wootton, 1992).

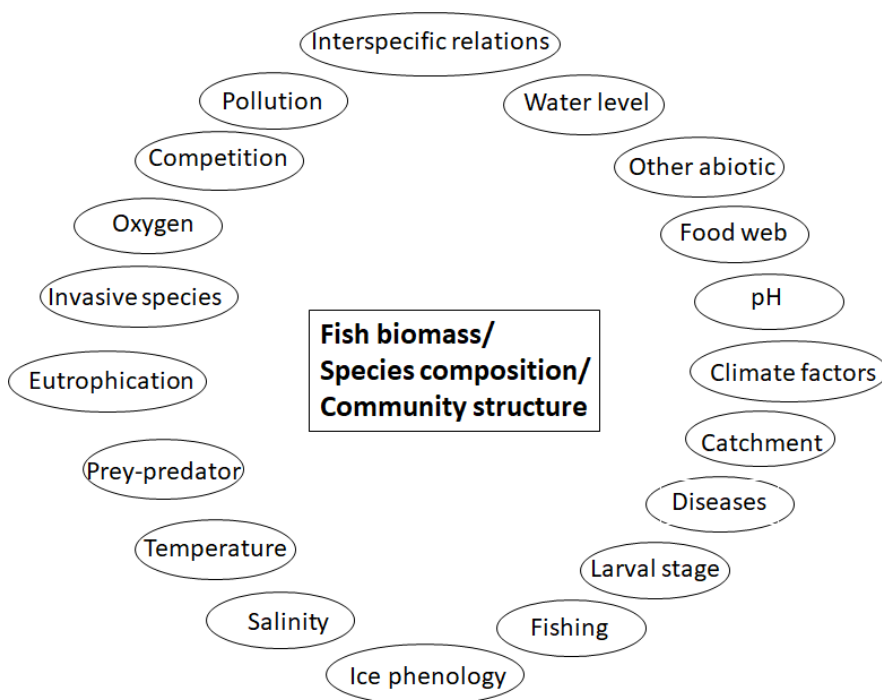


Figure 1. Schematic overview of the most frequent keywords in the literature regarding stressors/factors that affect fish biomass, composition, and community structure.

Understanding the joint effects and interactions of these factors/stressors on fish communities would help to predict ecological dynamics of lake ecosystems (Beisner et al., 2006; Cheng et al., 2010), however, it is not an easy task. For this reason, different modelling approaches have been used to determine the changes in fish biomass and population dynamic (Christensen and Walters, 2004; Cremona et al., 2018a; Methot Jr and Wetzel, 2013; Pauly et al., 2000; Thorson, 2020). Modelling of complex system like freshwater ecosystems is a great challenge due to numerous parameters/stressors playing important role at the whole ecosystem level or specifically for fish (Ficke et al., 2007). To understand and detect common patterns and multiple interactions, multivariate approaches and machine learning algorithms are increasingly used in ecosystem related modelling studies (Bianchi and Høisæter, 1992; Breiman, 2001; Feld et al., 2016; Gebrekiros, 2016; Leathwick et al., 2006; Trigal and Degerman, 2015). Ecosystem modelling of lakes allows to determine how multiple factors act simultaneously on community composition, biological productivity, and biogeochemical processes (Håkanson, 2009).

Among all economically valuable fish species, European eel, *Anguilla anguilla* (Linnaeus, 1758) is a remarkable species because of its complex life cycle, spawning location, migration ability, adaptation, and its ecological and economical values (Tesch, 2003). Eel is a catadromous species inhabiting a wide variety of habitats such as freshwater, marine and brackish waters, but spawning in the Sargasso Sea (Kangur and Turovski, 2003; Tesch, 2003). Because of inefficient fish passways for their migration to Sargasso Sea, it was reasonable to restock eel into lakes all around the Europe (Dekker, 2019; Dekker and Beaulaton, 2016). Freshwater eel population relies on stocking in most European lakes. European eel can adapt and survive in unfavourable conditions, yet its stocks have tended to decline during the last half century in Europe (Dekker, 2003, 2016; Tesch, 2008). Climate change, habitat loss, pollution, intensive fishing and migration barriers such as dams, weirs, and pumping stations can be some of the identified stressors/factors for the eel population decline (Dekker and Beaulaton, 2016). Eel is economically the most valuable fish in Estonia being 5 to 20 times more expensive than the other commercial fish species (Järvalt et al., 2004), however, eel population/catch tends to decline, especially during the last two decades, despite the restocking programme (III).

Fish and fisheries in Estonian lakes are of great importance for locals economically as well as in recreational aspect. Northern pike, *Esox lucius* L., pikeperch, *Sander lucioperca* (L.), common bream, *Abramis brama* (L.), eel, and Eurasian perch, *Perca fluviatilis* L. are among the most economically important species of lakes Võrtsjärv and Peipsi nowadays (Järvalt et al., 2004; Järvalt and Pihu, 2002; Kangur et al., 2002). However, fish assemblages, abundance, and economical value have changed in both lakes over time (Järvalt et al., 2004; Järvalt and Pihu, 2002; Kangur et al., 2020; Tammiksaar and Kangur, 2020). Despite a biomass increase in some warm-water fish species like bream (**II**), the biomass and commercial catches of economically and ecologically valuable cool-water fish such as vendace, *Coregonus albula* (L.), lake (dwarf) smelt, *Osmerus eperlanus* m. *spirinchus* Pallas., showed a gradual but significant decrease in both Peipsi and Võrtsjärv (**II**) (Kangur et al., 2013; Kangur et al., 2007a; Tammiksaar and Kangur, 2020). Both lakes exhibit also sporadic fish kills (Kangur et al., 2016; Kangur et al., 2005; Kangur et al., 2013). Fish kills occurred in Lake Peipsi mostly because of temperature extremes in summer and synergistic effect with eutrophication. Cool-water species like smelt and vendace are most affected (Kangur et al., 2013). However, eurytherm, bottom dwelling fish like ruffe (*Gymnocephalus cernuus* (L.)) and juvenile fish are also suffering from extreme environmental conditions such as low DO, high pH and low water level in Lake Peipsi and Võrtsjärv (Kangur et al., 2016; Kangur et al., 2005; Nöges et al., 2007). Beside the above mentioned reasons, the influence of cyanotoxins on the condition of fish cannot be neglected either (Chen et al., 2021; Kangur et al., 2005). Although the effects of single parameters are studied in Peipsi and Võrtsjärv, the complex interactions between biotic-abiotic factors/stressors affecting fish and fisheries have not been addressed in detail previously.

2. AIMS AND HYPOTHESES OF THE STUDY

This thesis focuses on understanding climate change impact on Estonian large lakes, especially on key fish species. Besides, we studied the relationships between fish and their environment to understand the effects of biotic-abiotic factors and the direct and indirect effects of climate change on selected fish biomass. Information is merged from three published articles and hypotheses are tested with the following aims:

Article I

We track climate change effects on lake surface water temperature (LSWT) in Lake Peipsi, its variations and seasonality by using daily LSWT data collected from 1950 to 2018. More specifically, we aim to 1) investigate, how the ice phenology has been affected, 2) determine the changes in the frequency of extreme thermal events, 3) detect the degree of randomness in LSWT values.

Article II

We analyse which ecological factors, including biotic (interspecific) relationships and abiotic (environmental) variables, are mainly controlling the dynamics of fish biomass in Lake Võrtsjärv. Following Jackson et al. (2001), our main working hypothesis was that abiotic variables were better predictors of fish species biomass than biotic variables considering Võrtsjärv as a large system.

Article III

We investigate the most important environmental factors/stressors and their effect on restocked eels in Võrtsjärv directly after restocking and later in their growing phase. The hypothesis was that the number of specimens restocked had the strongest influence on the yellow eel stocks. We asked what affects most the commercial yield, which indicates the stock size of eels 7 years after restocking when the age class becomes most prominent in the catches – the number of specimens restocked, the conditions at restocking or the conditions of the particular fishing year.

3. MATERIAL AND METHOD

3.1. Study area

Lake Peipsi and Lake Võrtsjärv were chosen as the study lakes in the present thesis (Fig. 2). Lake Peipsi (surface area 3555 km²) is the largest transboundary lake and the fourth largest lake in Europe (after Ladoga, Onego, and Vänern). Lake Peipsi is located south of the Gulf of Finland on the border of Estonia and Russia and consists of three parts with different sizes, stretching from north to south: L. Peipsi s.s., L. Lämmijärv and L. Pihkva. Lake Võrtsjärv is the largest inland lake in Estonia with a surface area of 270 km² and is situated in central Estonia. The lakes are interconnected by the Emajõgi River. Peipsi and Võrtsjärv are both unstratified eutrophic shallow lakes with average depths of 7.1 m and 2.8 m, respectively. Maximum depths of Peipsi and Võrtsjärv are 15.3 m and 6 m, respectively. Notable water level fluctuation is occurring in both lakes. Both lakes are belonging to the polymictic type of lakes meaning that full mixing of the water column occurs several times a year. Lakes are ice-covered on average 135 days during the winter (I, Nõges et al., 2010). Lake Peipsi and Lake Võrtsjärv are biologically highly productive lakes. The productivity of the lakes prompts to a high number of species in both lakes. Lake Peipsi and Lake Võrtsjärv are inhabited by 36 and 31 permanent fish species, respectively (Järvalt and Pihu, 2002; Järvalt et al., 2004; Tammiksaar and Kangur, 2020).



Figure. 2. Location of study lakes Peipsi and Võrtsjärv (Kangur et al., 2020)

3.2. Data collection and examination

Long term data was used for all the studies (**I**, **II**, **III**). Daily lake surface temperature from 1950 to 2018 was measured at Mustvee hydrometric station of Lake Peipsi which represents Lake Peipsi s.s. open water conditions (Lieberherr and Wunderle, 2018) (**I**). Measurements were taken from the surface layer of the water using Celsius mercury thermometer twice in 24 hours at 8 am and at 8 pm (Jaani, 2001). An automatic station was used for hourly LSWT measurement since May 2009. LSWT data were obtained from the Institute of Meteorology and Hydrology of the Estonian Ministry of Environment and Estonian Weather Service of the Estonian Environment Agency. Peipsi LSWT data was parametrised by using the raw daily LSWT, thresholds of 1°C and 17°C for high and low temperature, and a smoothed water temperature curve (Fig. 3) (**I**). Dynamic parameters were obtained from using the smoothed water temperature curve and yearly LSWT fluctuation. Ice-cover period was calculated as the period of water temperature continuously below 1°C and 17°C was chosen as the threshold for high temperature dues to its impact on the cool-water fish species like vendace (Potapova, 1978). Beside that, extreme high and low temperatures were calculated as

97.5th percentile (23.3°C) and 50th percentile (5.6°C) to investigate the frequency of the extreme events in the lake. Parameters were divided into 3 interval periods based on Wild Binary Segmentation for Multiple Change-Point Detection (1950-1972, 1973-2006 and 2007-2018; 0.05°C, 0.09°C, 0.5°C, respectively). Calculated water temperature parameters and definitions were given in Table 1 in article I.

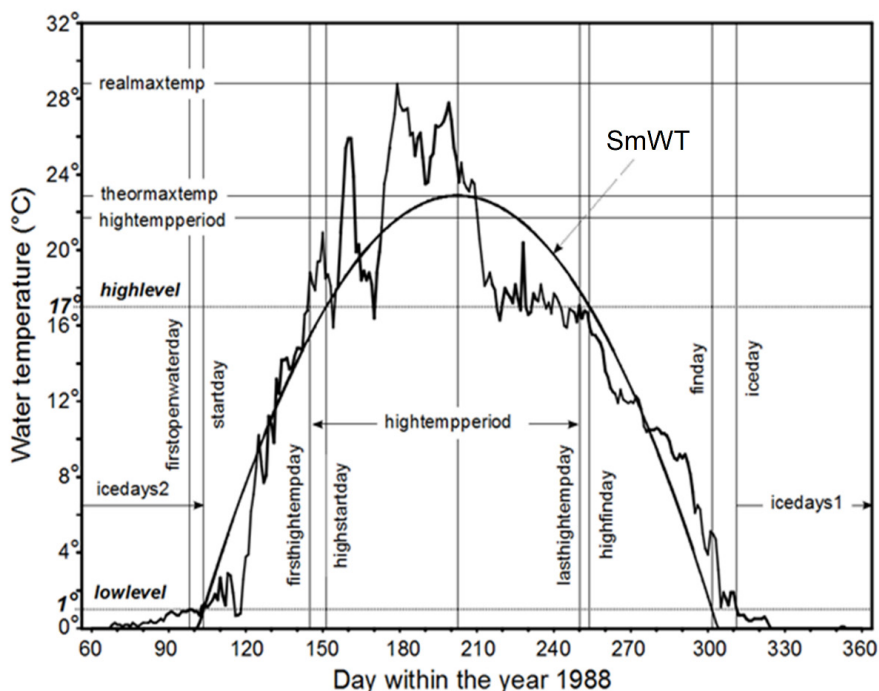


Figure. 3. Calculation of selected LSWT parameters and dynamic water temperature parameters using the smoothed water temperature curve (SmWT) fitted to daily water temperature. 1988 is selected as an example year and the same approach was applied to each year separately (I).

For Lake Võrtsjärv, LSWT data were measured by the Institute of Hydrology and Meteorology (presently Estonian Environment Agency). Monthly water chemistry analyses (TN , TP , PO_4^- , NO_3^- , HCO_3^-) were performed at the Tartu laboratory of the Estonian Environmental Research Centre according to the international (ISO) and Estonian (EVS-EN ISO) quality standards. Transparency of the water was measured with Secchi disk and portable electrochemical oxygen meter was used to measure DO concentration. Water level was measured by the Estonian Weather Service at the outflow of Võrtsjärv with the reference point at 33.01 m (II). The long-term monitoring station of

Lake Võrtsjärv for the water samples is representative of >90% of the lake area (58°12'40.0"N 26°06'20.0"E) (Nõges and Tuvikene, 2012). Water samples for phyto- and zooplankton and sediment samples for macroinvertebrates were collected on a monthly basis during ice-free period. Two type of Ekman grabs were used for sediment samples. Utermöhl (1958) method was used for the phytoplankton counting and biomass calculation.

Bottom otter trawl was used for fish catch during the ice-free period. The biomass proxy was calculated by WPUE (weight per unit effort), catchability and fishing effort (Nõges et al., 2016). Long term data was used covering the period from 1979 to 2016 (II). Pike, perch, pikeperch, ruffe, bream, and white bream (*Blicca bjoerkna* (L.)) have been selected for this study (II) due to their ecological and economical importance. More information on sample examination of Lake Võrtsjärv is available in Article II

Eel production in Lake Võrtsjärv entirely depends on restocking of glass eels or elvers because of the hydroelectric power station on the Narva River hindering natural migration. The restocking program started in 1956 (Kangur et al., 2002). Commercial eel catch data were used instead of biomass. Restocked elvers or glass eels are named young-of-the-year (YOY) and eels of the catch size are called yellow eels. Correlations between yellow eels (kg) and YOY (number of specimens restocked) were calculated while shifting the series by 0-12 years relative to each-other. A gap of 7 years was found to display the strongest correlation and the result was supported by the harvesting data showing that the 7-years age group was the most dominant in the catch (Fig. 4) (III).

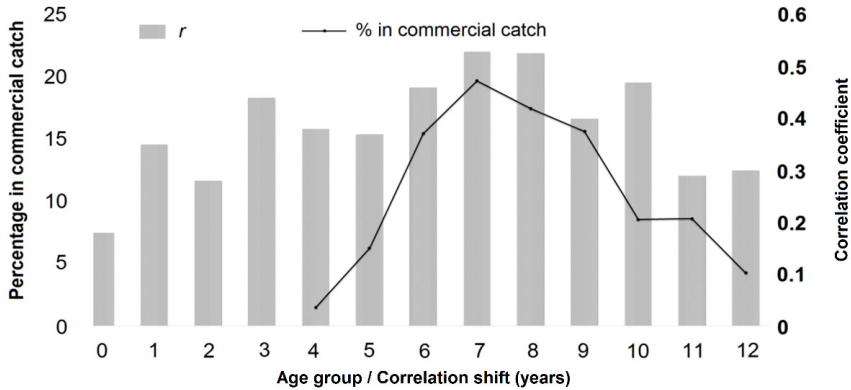


Figure 4. Coefficients of shifted (by 0-12 years) Pearson correlation between restocked YOY numbers and yellow eel catches (bars, scale on the right) and the distribution of age groups (kg) in the commercial catch (Bernotas and Silm, 2019) (line, scale on the left).

3.3. Data analysis

Data analysis was carried out using multiple packages of the R software (R Core Team, 2020). Peipsi water temperature data was split into three time period intervals selected by using the Wild Binary Segmentation for Multiple Change-Point Detection on winter LSWT by using R package *wbs* (Baranowski and Fryzlewicz, 2014). Descriptive statistics, ANOVA and *t*-tests were applied to detect significant changes during the study period. To detect trends in LSWT parameters, polynomial regression analysis was applied. The *stl* function was used to analyse the seasonal decomposition of the time series and to check randomness of the seasons and the whole temperature series (Cleveland et al., 1990) (**I**).

The Shapiro-Wilk test was used to test the normality of the data (**II**, **III**). Parameters with non-normal distribution were transformed to natural logarithm or logarithm (x+1). Variance Inflation Factor (VIF) was applied with the threshold set at 8 to detect collinearity among the parameters and to exclude those parameters from further analysis (Cremona et al., 2018b; Feld et al., 2016; Naimi, 2015; Zuur et al., 2007) (**II**, **III**). To determine the most influential predictors for each fish species biomass, three statistical approaches were applied. By using the R package *corrplot* (Wei and Simko, 2013), Pearson correlation coefficients were calculated to determine relationships between the factors and fish biomass/catch (**II**, **III**). To discover common pattern between

environmental variables and organisms' biomass, Co-inertia analyses (COI) was applied by using the R package *ade4* (Dray et al., 2007) (**II**, **III**). Finally, we employed the machine learning method Random Forest (RF, R package *RandomForestSRC*, Feld et al., 2016; Ishwaran and Kogalur, 2017) to select most important parameters for each fish species (**II**, **III**).

Models were constructed with additive and interaction effects by Generalised Least Squares (GLS) with the three best predictors derived from the result of correlation, COI and RF to estimate each fish biomass by using the R package *nlme* (Pinheiro et al., 2007) (**II**). Moran I test was applied to the residuals to test the temporal autocorrelation by using the R package *ape* (Paradis and Schliep, 2019) (**II**, **III**). No significant autocorrelation was detected. Akaike's Information Criterion AIC (Akaike, 1973) was used to evaluate the model performance, and dredge function was applied for automated model selection through AIC values by using R package *MuMIn* (Barton and Barton, 2015). Models with a delta AIC (ΔAIC) lower than 2 were considered equally supported (Burnham and Anderson, 2004) (**II**, **III**).

Generalised Linear Models (GLM) were used to estimate the yellow eel catch (kg) and YOY (number of the specimens) based on the four most important parameters that were revealed from RF. Model parameters were centered to be eligible for comparison. Due to small sample size, the small-sample equivalent of Akaike's Information Criterion (AICc) was used for evaluation and selection of the model (Akaike, 1973; Brewer et al., 2016) (**III**).

4. RESULTS

4.1. Parameterisation of lake surface water temperature data and trend detection in Lake Peipsi time series (I)

Changes in LSWT and SmWT parameters were investigated to determine the impact of climate change in Lake Peipsi. Significant changes (cubic regression) in LSWT occurred only in autumn and winter (Fig. 5c, d; $p < 0.05$ and $p < 0.001$, respectively). A dramatic increase in winter LSWT from 0.15°C to 0.63°C occurred since the 2000s. The highest average winter LSWT (1.2°C) was recorded in 2007 and the fluctuation increased again since that. However, the number of cold days ($\text{WT} < 5.6^{\circ}\text{C}$) was not affected by the increase of LSWT in winter in Peipsi, although ice-cover period decreased. Besides, annual LSWT was not affected by the significant changes in winter and autumn WT (Fig. 5). Approximately average two weeks delay was detected in ice formation from initial. There was no significant trend in epilog (days from temporary to permanent ice cover), however epilog in the last interval (2007-2018) showed significant increase compared to the other two intervals (Supplementary Table A.1, I).

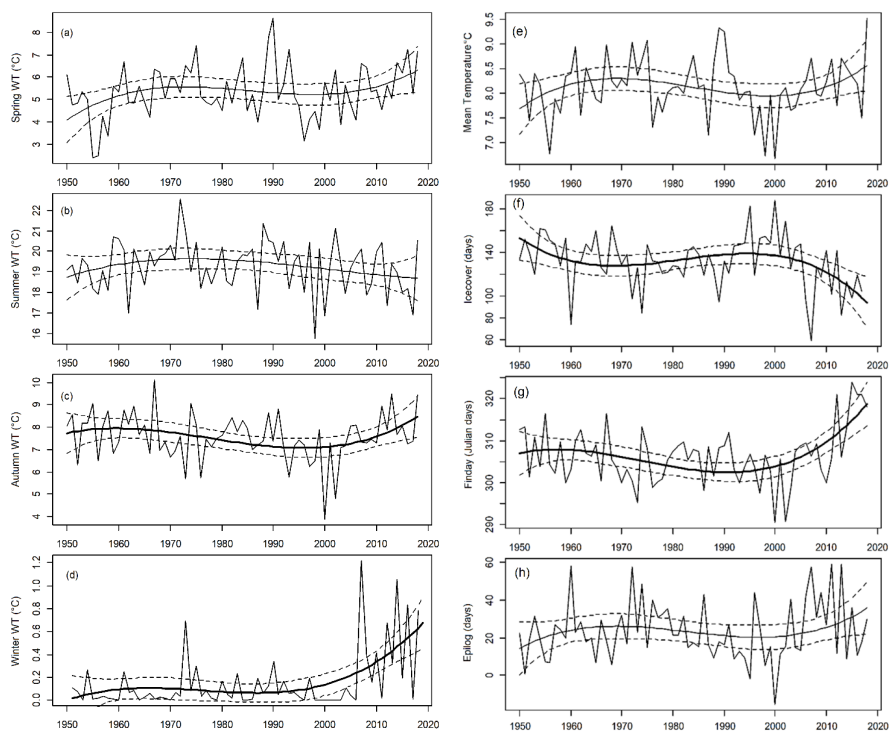


Figure 5. Long-term mean LSWT per season (a-d), annual mean LSWT (e), duration of the ice-cover period calculated from LSWT (f), Julian day of SmWT lower than 1°C termed “Finday” (g), and number of days between first ice phenomena and permanent ice cover (LSWT-SmWT) termed “Epilog” (h) in Lake Peipsi. Cubic regression curves (continuous line) with 95% confidence limits (dashed lines) predict the spread of parameter values over time (n=79). Bold continuous lines (panels c, d, f, g) indicate statistically significant trends ($p < 0.05$ for autumn LSWT, $p < 0.01$ for winter LSWT, duration of ice cover, and Finday).

Frequency of extremely hot and cold days (97.5th and 50th percentile, respectively) did not show any significant increase or decrease in recent years (Fig. 5 in I) and two out of five peaks of hot days were found in the last century. Parameter intervals for three periods (1950-1972, 1973-2006, 2007-2018) are given in Supplementary Table A.1 in article I. Most significant changes were found in winter related parameters such as ice phenology, days of ice cover and winter LSWT in the last period. Notably, warming in the last 45 days of the year and LSWT reaching an average of 1.25°C caused a delay of approximately 15 days in permanent ice formation in the last period (2007-2018).

Seasonal decomposition of spring, summer, autumn and whole year LSWT time series are given in Supplementary material (Figs. A.1–A.4, in article I). The remainder/noise was calculated by subtracting the seasonal and trend fit from the raw data and a significant increase in randomness was recorded in variance of winter LSWT since 2007 (Fig. 6).

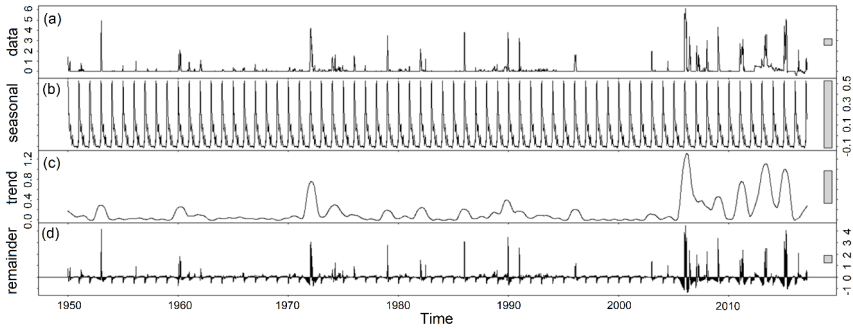


Figure 6. Seasonal decomposition of winter LSWT time series. Daily winter observed data (December, January, February) for 69 years (a), seasonal component (b), trend (c) and remainder of those three components (d). Bars on the right side of each graph show the relative magnitude of each component (I).

4.2. Relations between abiotic-biotic factors and selected fish biomasses in Lake Vörtsjärv (II)

Excluding mechanistically related variables like phytoplankton and cyanobacteria, the strongest correlation was found between HCO_3^- and white bream (Fig. 7; $r = 0.64$, $p < 0.001$). Pike correlated positively with two other fish species – pikeperch ($r = 0.37$, $p < 0.001$) and perch ($r = 0.46$, $p < 0.001$), and negatively with summer temperature ($r = -0.31$, $p < 0.05$). Significant correlations for pikeperch were found with bream ($r = 0.37$, $p < 0.05$), summer temperature ($r = 0.33$, $p < 0.05$), water level ($r = 0.32$, $p < 0.05$), phytoplankton ($r = -0.45$, $p < 0.001$), cyanobacteria ($r = -0.51$, $p < 0.001$), and the proportion of cyanobacteria in phytoplankton (cyan/phy) ($r = -0.42$, $p < 0.001$). Significant correlations for the bream were with white bream ($r = 0.42$, $p < 0.001$), ruffe ($r = 0.40$, $p < 0.05$), benthic macroinvertebrates ($r = 0.36$, $p < 0.05$), summer temperature ($r = -0.42$, $p < 0.001$) and cyan/phy ($r = -0.40$, $p < 0.05$), while for white bream were perch ($r = 0.41$, $p < 0.001$) and ruffe ($r = 0.36$, $p < 0.05$) and for ruffe were perch ($r = 0.58$, $p < 0.001$) and benthic macroinvertebrates (BMI; $r = 0.40$, $p < 0.05$).

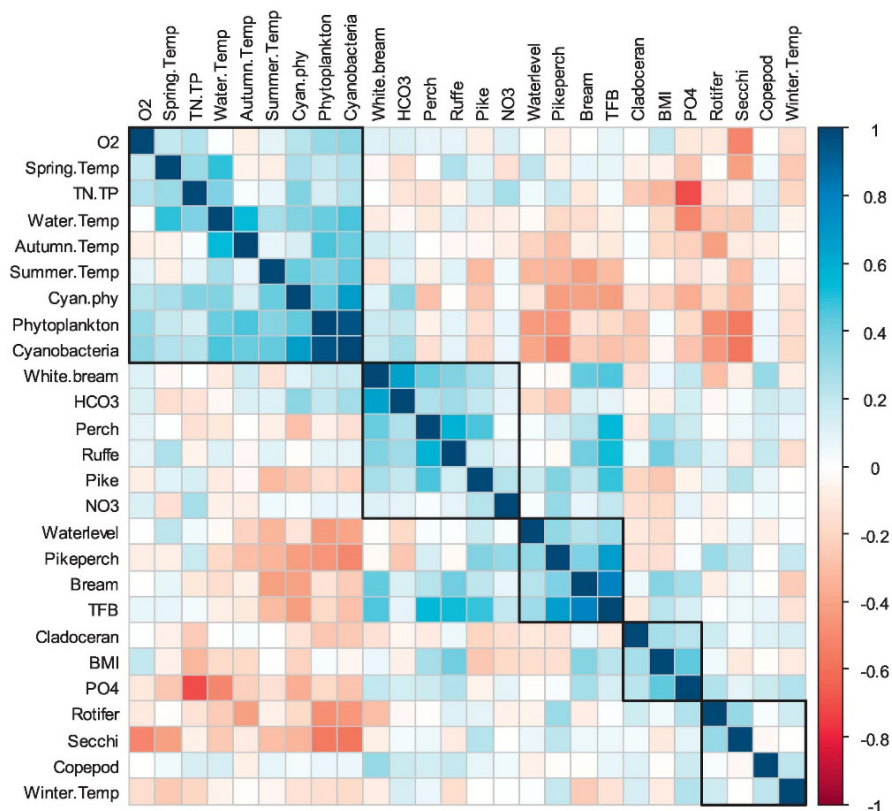


Figure. 7. Pearson correlations between fish biomasses and ecological variables. Strength of the relationships (correlation coefficients) is given in colour according to the scale at the right side of the panel ($n=37$). Blue shades show positive correlations while red shades represent negative correlations. Variables are ordered according to hierarchical clustering and clusters of strongly positively related variables are framed.

In the co-inertia analysis (COI), the first two axes explained 75.5% of the variance with a moderate strength of the relationship (Fig. 8; $RV = 0.34$, $p < 0.001$). According to the pattern, increase in temperature-related parameters (except winter temperature) was likely causing the increase in phytoplankton and cyanobacteria, and decrease in rotifers, pike and pikeperch. Biomasses of white bream, ruffe, perch, BMI and bream tended to decrease in conditions of high TN/TP and high winter water temperature. NO_3 was the least significant among the abiotic factors in the COI test.

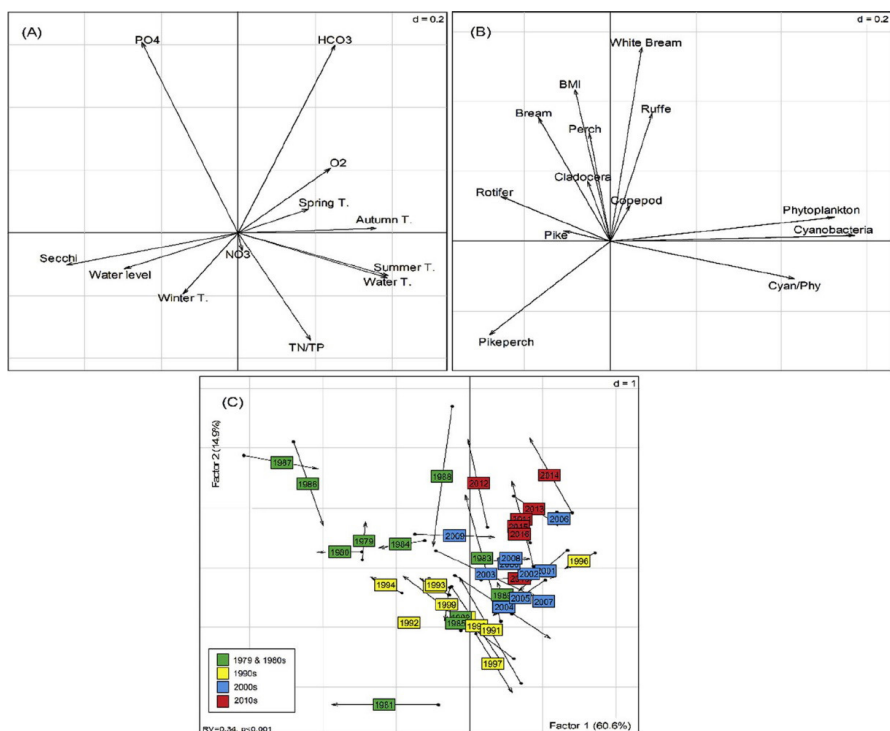


Figure 8. Co-inertia analysis of the environmental variables (A) and organism biomasses (B); the length and direction of vectors denote the weights of the variables in the first two factors. Panel C represents the concordance between environmental parameters and biomasses for different years ranging from 1979 to 2016. The anterior and posterior part of the arrows denote the relative location of samples according to environmental parameters and biomass values, respectively; the numerical measure of concordance is given by the RV-coefficient, for which p -value is evaluated by permutation test; percentages indicate the proportion of the overall covariance described by the first two factors.

In the last test for pre-selection of variables, the importance of the predictor variables for each fish species biomass was ranked by the RF model (Fig. 9). For the top predator fish species like pike and pikeperch, nutrient related parameters such as TN:TP, NO_3 were important. However, we did not take NO_3 into account due its to insignificant weight in COI and Pearson correlation analysis. Temperature-related parameters and cyanobacteria were influential predictors for most of the fish species.

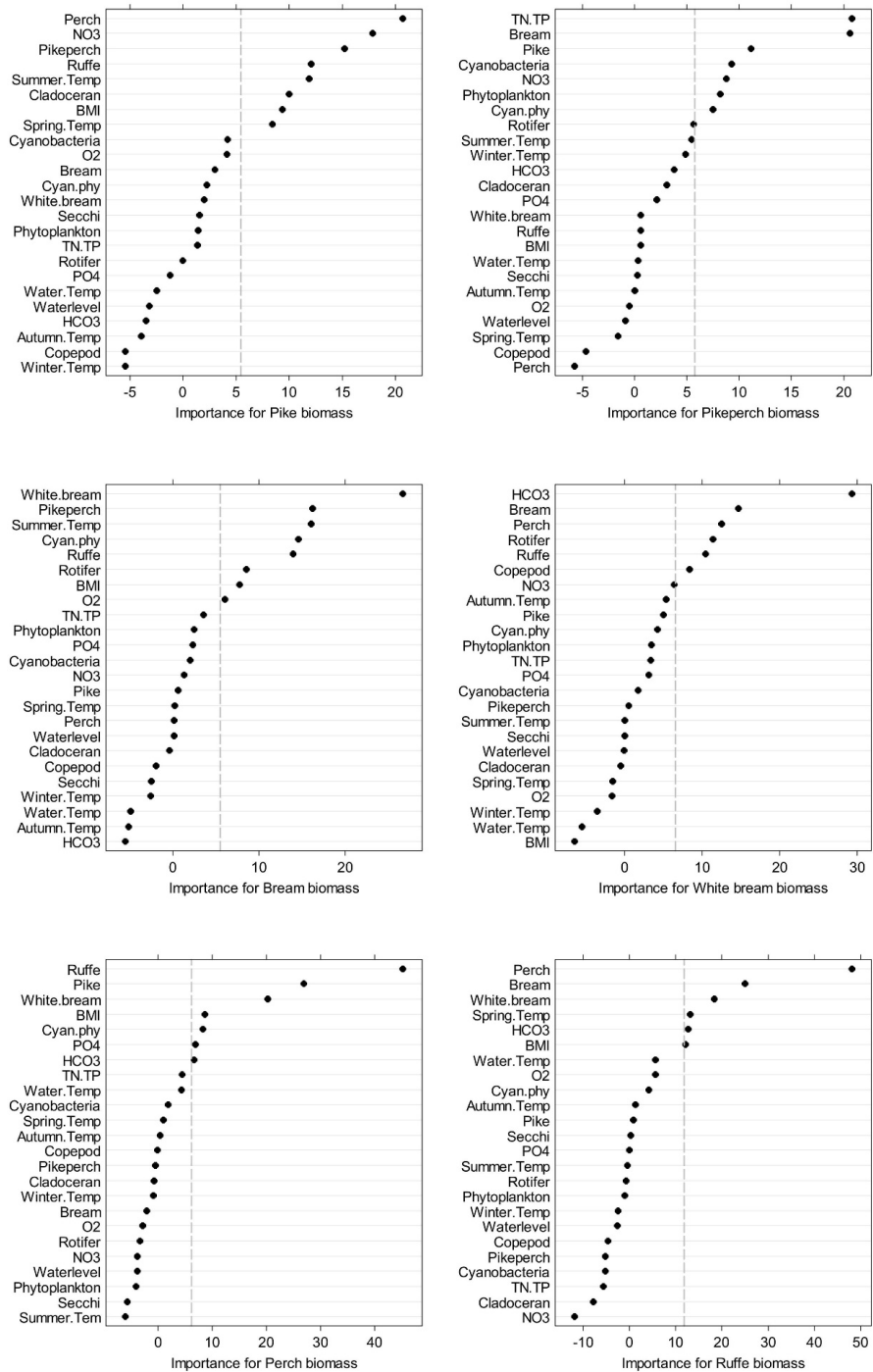


Figure. 9. Importance ranking of explanatory variables for six fish species by Random Forest model. Variables reaching the right side of the vertical dashed line have high predictive capacity, whereas the others are irrelevant for the response variables (II).

GLS models were run with the three pre-selected predictors revealed by the three different tests for each fish species (Table 1). Best models (additive or interactive) for each fish species were selected according to AIC values (supplementary material Table 1 in article II). Selected models could explain 40% to 60% of the fish biomass variance by selected parameters (Fig. 6 in article II). Additive effect used to explain pikeperch and bream biomasses. For perch and white bream, predictors with interactive effects obtained the best AIC, while a combination of interactive and additive effects performed best for ruffe and pike.

Table 1. Generalised Least Squares models for biomasses of fish species based on selected explanatory variables (II)

<i>Model Number</i>	<i>Response variables</i>	<i>Model</i>	<i>AIC</i>	<i>df</i>	<i>R²</i>
<i>Mod1</i>	Pike	$\log(B_{\text{Pike}}) = \log(B_{\text{BMI}}) + \log(B_{\text{Perch}}) * \log(\text{Summer Temperature})$	75.4	7	0.45
<i>Mod2</i>	Pikeperch	$\log(B_{\text{Pikeperch}} + 1) = \log(\text{TN/TP}) + \log(B_{\text{Bream}}) + \log(B_{\text{Cyanobacteria}})$	51.4	5	0.43
<i>Mod3</i>	Bream	$\log(B_{\text{Bream}}) = \log(B_{\text{Pikeperch}}) + \log(\text{Summer Temperature}) + \log(B_{\text{BMI}})$	26.1	5	0.4
<i>Mod4</i>	White bream	$\log(B_{\text{White bream}}) = \log(\text{HCO}_3^-) * \log(B_{\text{Rotifer}}) * \log(B_{\text{Perch}})$	99.7	9	0.59
<i>Mod5</i>	Perch	$\log(B_{\text{Perch}}) = \log(B_{\text{Ruffe}}) * \log(\text{cyan/phy}) * \log(B_{\text{White bream}})$	84.1	9	0.60
<i>Mod6</i>	Ruffe	$\log(B_{\text{Ruffe}}) = (\log(B_{\text{BMI}}) + \text{Spring Temperature}) * \log(\text{HCO}_3^-)$	107.6	7	0.41

4.3. Environmental factors explaining yields of European eel in Lake Vörtsjärv (III)

Correlation coefficients were used to evaluate the single relationship among the yellow eel, YOY eel and their environments. For YOY, strong negative correlations were found with cyanobacteria biomass ($r = -0.69$, $p < 0.001$) and total phytoplankton biomass ($r = -0.59$, $p < 0.05$) and a positive correlation with summer temperature ($r = 0.43$, $p < 0.05$) (Fig. 10A). Most significant correlations for commercial yield of yellow eel were found with biomasses of metazooplankton ($r = 0.39$, $p < 0.05$), phytoplankton ($r = -0.36$, $p < 0.05$), cyanobacteria ($r = -0.34$, $p < 0.05$), autumn water temperature ($r = -0.33$, $p < 0.05$) and total phosphorous concentration ($r = 0.38$, $p < 0.05$) (Fig. 10B).

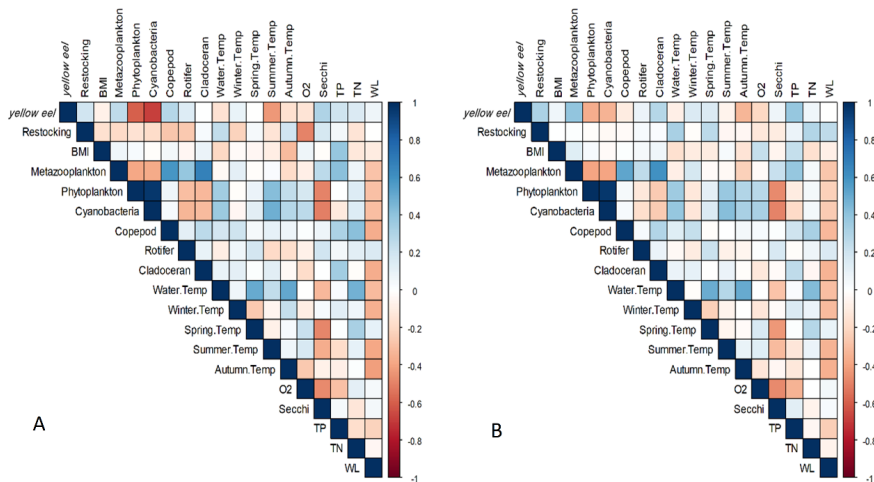


Figure 10. Pearson correlation between commercial eel yield and environmental variables during the YOY stage (7 years before the catch; A) and in the year of catch (yellow stage; B). Strength of the relationship (correlation coefficients) is given in colour on the right side of the panel. Blue gradients indicate positive correlations and red gradients negative correlations (III).

Random Forest (RF) tests revealed that the most important parameters for YOY were cyanobacteria, summer temperature and copepod biomass beside restocking, while the most important parameters for yellow eel were nutrients (TP and TN), metazooplankton and restocking (Fig. 11).

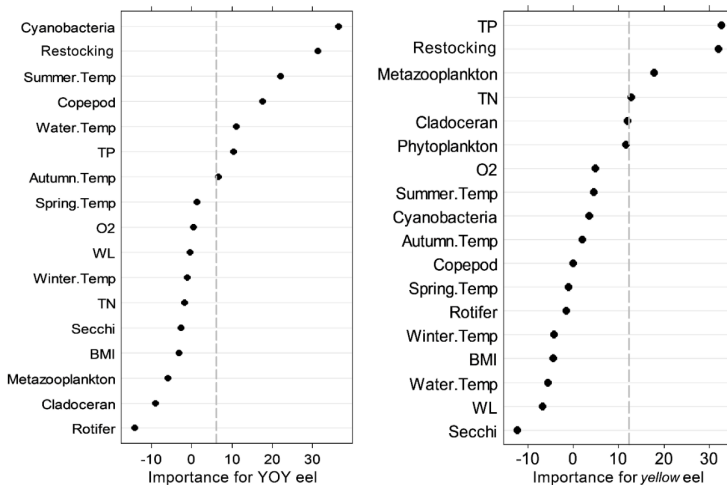


Figure 11. Importance ranking of explanatory variables for commercial eel catch by Random Forest model: Left panel - during YOY stage (7 year before catch) and Right panel – during yellow stage (in the year of catch). Variables reaching the right side of the vertical dashed line have high predictive capacity, whereas the others are irrelevant for the response variables – YOY and yellow eels (III).

The pre-selected by RF predictors were further used to construct Generalised Linear Models (GLM) for both YOY and yellow eel with additive and interaction effects. Neither models showed significant temporal autocorrection. R^2 varied from 0.56 to 0.78 for YOY and from 0.54 to 0.64 for yellow eel that are within the range of $\Delta AICc < 2$ (5 models for each YOY and yellow eel). All the other models are given in Supplementary Table 1 in article **III**. Selected models for YOY and yellow eel are given in Table 2 with the selected parameters.

Table 2. Best Generalised Linear Models for eel catches based on restocked number and conditions during YOY and yellow stages (**III**).

<i>Stage</i>	<i>Model equation and parameters</i>	<i>AIC</i>	<i>df</i>	<i>R²</i>
<i>YOY</i>	Eel \sim Copepod*(0.357) + Cyanobacteria*(-0.668) + Stocking*(0.170) + (5.8*10 ⁻¹⁶)	65.55	5	0.59
<i>Yellow</i>	Eel \sim Metazooplankton*(0.239) + Stocking *(0.168) + TN*(0.240) + TP*(0.167) + Metazooplankton:TP*(0.295) + TN:TP*(-0.423) - 0.118	94.5	8	0.56

5. DISCUSSION

5.1. Lake surface water temperature and ice phenology respond to climate change

Rising trends in water temperature of lakes are commonly acknowledged in the literature as a consequence of global warming. However, lakes at different latitudes show different responses to climate change (O'Reilly et al., 2015). Responses of lakes may vary according to lake type, size, and location. Recent studies showed that while some lakes show increasing trend in water temperature, some others tend to cool down (O'Reilly et al., 2015). Changes in water temperature in tropical and subtropical lakes mostly occur in summer (rise), while winter temperature is the most affected period in Northern Hemisphere lakes (O'Reilly et al., 2015). Changes in the yearly LSWT of Peipsi were insignificant over the last decades (I), however, winter was the most affected season by climate change, with the year 2007 being the break point (3. wbs period starts) for winter related parameters (I). Lake Ladoga, Europe's largest lake located at ~ 480 km distance from Peipsi shows similar warming trend since 2007 (Karetnikov and Naumenko, 2011). Many other studies also recorded upward trend in winter lake temperature, especially in the Northern Hemisphere (Carvalho and Kirika, 2003; Delju et al., 2013; Kirillin, 2010) where winter air temperature is controlled by North Atlantic Oscillation (NAO) (Hurrell, 1995; Jennings et al., 2000; Wrzesiński et al., 2015; Wrzesiński et al., 2018). It has been reported that winter air temperature in Estonia is under the influence of NAO through wind direction and intensity (Jaagus and Kull, 2011). Decomposing the LSWT data revealed an increase in winter LSWT randomness due to strong fluctuations in this variable after the year 2007 (I).

Most of northern lakes are ice covered in winter. Ice cover is a sensitive indicator for changes in global and local climate (Brown and Duguay, 2010; Cheng et al., 2014; Karetnikov and Naumenko, 2007). It is reported that the ice cover duration sensitively reflects the changes in local air temperature in the Peipsi region (Nõges and Nõges, 2014). Ice cover period is an important factor for thermal moderation, energy exchange, and atmospheric gas exchange of the lake as well as for the organisms adapted to live in cold-water systems (Brown and Duguay, 2010). Changes in ice phenology can be crucial for cool-water species

like vendace, burbot and smelt (Kangur et al., 2020). Changes in winter water temperature (as a covariant of the winter air temperature) can interrupt the ice cover period and lead to delay in ice formation. In Peipsi, it occurred that temperature fluctuation or increase at the beginning of winter lead to a delay of ~15 days in the formation of permanent ice cover compared to long-term (1950-2018) average (I). Such shift might affect the whole ecosystem by changing fish spawning period, feeding habits, and increase the chance of algal bloom (Farmer et al., 2015; Lenard et al., 2019; Watz et al., 2016). Late ice formation and early break-up in Lake Peipsi extended the open water period (I), however, it did not lead to an increase in the mean open water temperature because of cool temperatures right before the ice-on and right after the ice-off. Shorter ice cover and longer ice-free period might cause changes also in the composition on phyto- and zooplankton communities (Shimoda et al., 2011) that can impact fish via food web (Jeppesen et al., 2010a). Additionally, temperature and photoperiod control life history events (spawning, hatching, larval emergence) for most of the fish species (Farmer et al., 2015; Hewitt et al., 2018; Preston and Rusak, 2010). Changes in winter temperature and ice phenology can shift the timing of those events (promote early hatching or early spawning for some species) that can lead to mismatch between the occurrence of fish larvae and their prey (Farmer et al., 2015). Earlier spawned species can benefit and be successful in competition with other, disadvantageous, larval stage fish and also adult warm-water species can get an advantage against cold- and cool-water fish species (Jeppesen et al., 2010a; Shuter et al., 2012).

5.2. Fish biomass is driven by climate, eutrophication and food web interactions

Environmental factors, including food web interactions that are affecting fish and fisheries, have been intensively studied over the last decades with modelling approaches (Bhele et al., 2020; Cremona et al., 2018a; Guo et al., 2019; Knack et al., 2020; Salman et al., 2019). Getting a clear picture of the climatic effects on fish is challenging due to direct and indirect effects and complex interactions. Seven economically and ecologically most important fish species were investigated in this thesis to understand fish to fish and environment to fish relationships. For six fish species (pike, pikeperch, perch, bream, white bream, ruffe) biomass was used as the response variable for both abiotic and biotic factors

including other fish species (II). For eel, commercial fisheries data were used with biotic-abiotic parameters and additionally eel stocking data (III). Outcomes of the GLS showed that additive effects or interactions could explain 40% to 60 % of the changes in fish biomass with selected parameters (II).

Food availability, prey-predator relationship, competition and other interspecific interactions are strongly influencing fish populations and assemblages in freshwater systems (Chase et al., 2002; Hanson and Leggett, 1986; Quintana et al., 2015). RF results revealed that for some species like ruffe, interspecific relationships (with bream, white bream and perch) were more important than environmental factors (II). It is known that ruffe competes for food with bream due to low chironomid larvae biomass in Lake Võrtsjärv in summer (Järvalt et al., 2004; Kangur et al., 1999) and that ruffe preys on larvae of other fish species in Estonian lakes (Saat et al., 2003). It has also been reported that ruffe competes with yellow perch (*Perca flavescens*), trout perch (*Percopsis omiscomaycus*) and other native benthivorous fish for food in North America (Fullerton et al., 1998; McLean, 1993; Ogle et al., 1995; Raloff, 1992; Savino and Kolar, 1996) and is similarly able to compete for food resource with native perch in Estonian lakes. BMI interaction with ruffe can be explained by soft-bodied macroinvertebrates being a preferred food resource for ruffe (Fullerton et al., 1998; Ogle et al., 2004), especially *Chironomus plumosus*, in both large Estonian lakes (Kangur et al., 1999). The strong relationship between bream and BMI is based on the predominantly benthivorous feeding type of bream (II). Ruffe and perch are among the preferred prey items for pike and pikeperch (Järvalt et al., 2004; Kangur et al., 2007b). RF results revealed that biomasses of perch and bream are strongly related to biomasses of pike and pikeperch, respectively. This relationship may possibly be less relevant for smaller pikeperch individuals which cannot feed on deep-bodied bream due to the mouth gap limitation (Didenko and Gurbyk, 2016; Dörner et al., 2007). Because of that, relationships between bream and pikeperch might be caused by the similarity of ecological requirements (warm and eutrophic water) for these two species (Kangur et al., 2020; Kangur et al., 2007a; Sandström and Karås, 2002). Although rotifers are dominant zooplankton group in Lake Ladik, they are the least preferred prey choice by white bream (Yağci et al., 2015; Yazıcıoğlu et al., 2017). High abundance of small zooplankters like rotifers may hint to poor condition for white bream and, thus, may be the reason for the negative relationship found between

rotifers and white bream biomass. Biomasses of other fish species were more influential factors for the biomass of perch compared to environmental factors (II). Perch can tolerate a wide range of ecological conditions such as low oxygen, low pH, and high organic matter content (Ojaveer et al., 2003; Rask, 1983). Additionally, perch diet can vary and consist of zooplankton, macroinvertebrates and (for larger individuals) fish (Ojaveer et al., 2003; Rask et al., 2014). Therefore, biotic factors had a greater influence for perch than abiotic factors.

Abiotic factors such as spring and summer temperature, TN/TP and HCO_3^- were the most important environmental parameters to explain biomass changes of the six fish species (pike, pikeperch, ruffe, perch, bream, white bream) (II). Bream is highly tolerant to a large range of temperature changes (Lehtonen, 1996). Oxygen depletion, water level decrease and cyanobacterial blooms during heat waves might be the reason for the observed negative relationship between bream and summer temperature. Spring temperature is one of the crucial parameters that can affect spawning time and warm springs might be favourable for ruffe spawning (Brown et al., 1998). Relationship between pikeperch biomass and TN:TP ratio can be explained by high TP concentrations leading to cyanobacteria growth that is detrimental to piscivores fish (Jeppesen et al., 2012). BMI are not among the food sources for adult pike, but rather for pike fry (Ojaveer et al., 2003). High abundance of BMI might be advantageous for pike fry, thus for pike in general. Pike is considered a moderately cold tolerant fish (Paaver and Lõugas, 2003). Negative relationship between summer temperature and pike can be explained by optimal temperature for young and adult pike being around 19°C and 22-23°C, respectively (Casselman, 1996). So, higher temperature might lead to negative growth for pike, and even cause summer fish kills linked to hypoxia (Kangur et al., 2005; Kangur et al., 2013). Some researchers have reported that the effect of water warming on fish is highly depending on body size (Vindenes et al., 2014). Besides, impact can occur also through the affected prey populations (Winfield et al., 2008).

Cyanobacterial toxic effect on fish and heavy blooms of cyanobacteria were not observed in Lake Vörtsjärv. A possible explanation for the negative relationship between the proportion of cyanobacteria in phytoplankton and total fish biomass might be explained by the long-term effect cyanobacterial domination on the food web (bottom-up

effect) and the episodic blooms in the lake that may cause a decrease in recruitment (Cremona et al., 2018a; Zhang et al., 2013). In addition, decomposition of poorly edible cyanobacteria can cause hypoxic conditions in the shallow lake in late winter (Havens, 2008; Kangur et al., 2005).

5.3. Impact of climate and other environmental factors on commercial yield of restocked European eel

GLM results showed that 59% of the variability in YOY survival and 56% in the harvest rate of restocked eel could be explained by the restocked number and environmental parameters (III).

According to literature, fish in the early life stage are under strong influence of the environment (Rijnsdorp et al., 2009). Therefore, investigating the YOY eel after being restocked to a water body bears great importance due to their vulnerability to new environmental stressors and growth conditions during the first lake year (III). The most important parameter for YOY eel was found to be the prevalence of cyanobacteria in the lake. Restocking the YOY to the lake takes place in spring at the time of rapid growth of cyanobacteria that can reach the peak in Lake Vörtsjärv in the middle of summer (Nöges et al., 2004). Reasons for the negative cyanobacterial effect on YOY eel might be that cyanobacteria can form on the littoral areas where eels cannot use it a sheltered habitat (Malbrouck and Kestemont, 2006). Abundance of cyanobacteria can impact the food source of eel prey, e.g. it may lower the abundance of the prey items of eel such as cladocerans (Ghadouani et al., 2003; Gliwicz, 1990). Relationship between YOY eel and copepods might be based on the fact that copepods are intermediate host for swim bladder parasite *Anguillicoloides crassus* and eels can be infected by feeding on them (Hubbard et al., 2016; Kirk, 2003; Nimeth et al., 2000). Additionally, body mass and length of the eels infected by *A. crassus* are greater than those of uninfected eels of same age (Lefebvre et al., 2013). Studies show that more than 50% of eels caught from Lake Vörtsjärv by passive fishing gear are infected (Bernotas and Silm, 2019; Kangur et al., 2010).

Fishing effort and fish abundance are components of the catchability, that means – the effectiveness of fishery (Arreguín-Sánchez, 1996). However, because of constant fishing effort in Lake Vörtsjärv (Järvalt

et al., 2004), the catchability can be described by the abundance of fish (III). Literature suggests that the catchability can be influenced also by environmental factors and fish behaviour (Hilborn and Walters, 2013; Hubert et al., 2012; Rogers et al., 2003). Nutrient related parameters and metazooplankton were the most important factors for the yellow eel catchability in Lake Vörtsjärv (III). Studies indicated that in aquatic systems controlled by bottom-up mechanisms, changes in nutrient concentrations are cascaded to higher trophic levels (Benndorf et al., 2002; Frau et al., 2019). In Lake Vörtsjärv, the food web structure is mostly controlled by bottom-up effects (Cremona et al. 2018a; Bhele et al., unpublished). Positive relations between eel and metazooplankton on one side, and eel and nutrients on the other side might indicate the bottom-up effect. As fyke net as a passive fishing gear was used for catching eel, yield success depends on fish movement (III). Therefore, high TP concentrations might stimulate eel movement by providing more organic matter throughout the food web.

6. CONCLUSIONS

The main objective of this thesis was to find general driving factors, including climate change impact, for fish and fisheries in Estonian large lakes.

Our results showed that both shortened ice cover period of Lake Peipsi and increase in winter LSWT occurred as a result of climate warming, although without any significant change on annual average LSWT. This resulted in an extension of the open water period since the beginning of the last century. Fluctuation in winter LSWT caused greater unpredictability and posed threat on beginning of the ice cover period. Although there was no increase in the frequency of extreme temperature events from 1950 to 2018, the consequences of the on-going winter warming and changes in ice cover phenology can be crucial for Lake Peipsi biota and ecosystem functioning. Besides, ecosystem service provisioning (ice fishing, ice roads) for local populations may become susceptible by weaker ice cover (I).

The proportion of cyanobacteria in total phytoplankton biomass was the only significant (negative) predictor for total fish biomass in Võrtsjärv. However, the influence of ecological factors on the biomass of individual fish species differed. For example, increase in water temperature may be detrimental to economically or ecologically important fish species and, at the same time, favourable for less valuable or warm-water species. This might cause shifts in the fish community and undermine ecosystem services provided by the lake, such as commercial fishing. Most effective abiotic factors such as TN:TP, HCO_3^- , summer and spring water temperature and interspecific relationships should be taken into account for future stock assessments and management planning of the lake. We conclude that biotic factors are as important as the abiotic factors for fish biomass in Lake Võrtsjärv (II).

Eel yield in Võrtsjärv was rather determined by the stressors and environmental factors in the lake during restocking time than the environmental factors during the year of harvest. Fish landing presents quite well actual biomass because of steady fishing effort in Lake Võrtsjärv where the number of fishing gear is constant. Based on the results of our study, we can conclude that although the number

of specimens restocked had strong influence on the yellow eel stocks then cyanobacteria biomass was even stronger parameter affecting the eel yield. Those two are followed by other food web components and nutrients, which may vary between different water bodies. However, the factors found in this study might help to optimise future eel restocking **(III)**.

Although winter is one of the most affected seasons by climate change in this region, the selected fish species and eel fishery in Estonian large lakes were more sensitive to other environmental stressors. However, since the changes in winter surface water temperature and ice phenology can affect other parameters, the indirect effect should not be ignored. Environmental factors/stressors can directly or indirectly interrupt ecosystem functioning and, with the increase in cyanobacteria, cause a degradation the system. Eventually, the impact on fish and fisheries may occur via affected food web components in the lake. The impact of factors can occur subsequently in fish communities and may lead to irreversible consequences, whereas the effects of concurrent climate change and eutrophication can mutually reinforce their symptoms.

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SUMMARY IN ESTONIAN

KLIIMAMUUTUSTE JA TEISTE ÖKOLOOGILISTE TEGURITE MÕJU VALITUD KALALIIKIDE POPULATSIOONIDELE JA KALAPÜÜGILE EESTI SUURJÄRVEDES

Järved on ühed kliimamuutuse poolt kõige haavatavamad ökosüsteemid. Paljud järved soojenevad isegi kiiremini kui ookeanid või atmosfääri õhk (Woolway et al., 2020). Kliimamuutuse mõju järvedele ilmneb kiiresti ning selle kõige tüüpilisemaks füüsikaliseks tagajärjeks on pinnavee soojenemine ning jääkate õhenemine ja lühenemine, eriti põhjapoolkera järvedes. Suured madalad järved nagu Peipsi ja Võrtsjärv peegeldavad kiireid muutusi õhutemperatuuris. Vee vähese kihistumise ja suure pindala-ruumala suhte tõttu on need järved ühed väliste tegurite (nt kliimamuutuse) poolt enim mõjutatud ökosüsteemid (Jeppesen et al., 2009; Moss et al., 2009; Nöges & Nöges, 2014). Üks olulisemaid kliimategureid põhjapoolsete järvede jaoks on muutused talvise õhutemperatuuris, mis võivad halvendada veekvaliteeti ja elupaiku ning vähendada kalatoodangut. Samuti võimendab kliimasoojenemine eutrofeerumise ilminguid järvedes (Jeppesen et al., 2010b). Kliimasoojenemise kaudsed mõjud võivad ilmneda liikide omavahelistes suhetes toiduvõrgustikus, sealhulgas sinivetikate osakaalu suurenemises fütoplanktonis (Cremona et al., 2014; Jeppesen et al., 2013). Lisaks kliimale võivad teisedki biotilised ja abiotilised tegurid, näiteks lahustunud hapniku sisaldus vees, ülepuük, haigused ja invasiivsed liigid mängida olulist rolli kalade biomassi, koosluse liigilise koosseisu ja struktuuri kujunemisel (Wootton, 1992).

Töö põhieesmärk on hinnata kliimamuutuse mõju Eesti suurjärvedele ning selgitada kalade ja nende elukeskkonna vahelisi seoseid. Sel eesmärgil uuriti biotiliste ja abiotiliste tegurite ning kliimamuutuste otsesest ja kaudset mõju valitud kalaliikide biomassile Eesti suurjärvedes.

Peamised eesmärgid on:

1. Selgitada kliimamuutuse mõju Peipsi pinnavee temperatuurile, selle pikaajalistele muutustele ja sesoonsusele. Täpsemalt uurida muutusi jääkate fenoloogias ja äärmuslike veetemperatuuride

esinemissageduses, samuti juhuslikkuse osa pinnavee temperatuuri varieerumises.

2. Teha kindlaks peamised ökoloogilised tegurid, sealhulgas biootilised (liikidevahelised) suhted ja abiootilised tegurid, mis kontrollivad kalade biomassi dünaamikat Võrtsjärves.
3. Teha kindlaks keskkonnategurid, mis mõjutavad kõige enam noorangerjaid kohe pärast asustamist Võrtsjärve ja kasvufaasis ning seeläbi angerjasaagi suurust.

Peipsi veetemperatuuri pikaajaliste ja sesoonsete muutuste uurimiseks kasutati Mustvee hüdrometriaajaama pinnavee temperatuuri igapäevaseid andmeid aastatest 1950-2018. Statistiliste meetoditega (kirjeldav statistika, aegridade analüüs) analüüsiti Peipsi järve pinnavee temperatuuri aastast muutlikkust ja sesoonsust ning hinnati pikaajalisi suundumusi, samuti tuvastati äärmuslike veetemperatuuride esinemissageduse muutusi ligi seitsme aastakümne jooksul (I). Ökoloogiliste tegurite mõju selgitamiseks kaladele kasutati Võrtsjärvest kogutud kalade biomassi ja keskkonnaseire andmeid aastatest 1979-2016. Tugevaimad ennustavad muutujad valiti kolme paralleelse lähenemisviisi abil: ühekordne korrelatsioon (Pearson), mitmemõõtmeline meetod (koinertsusanalüüs) ja masinõppe algoritm Juhumetsad (*Random Forest*), millele järgnes üldistatud vähimruutude mudel (GLS), et selgitada välja nende seos kalade biomassiga. Konstrueeriti mudeleid, millel oli nii aditiivne kui ka interaktiivne mõju (II). Võrtsjärve angerjamajanduse edukust mõjutavate keskkonnaparametrite selgitamiseks kasutati noorkalade asustamise andmeid alates aastast 1956 ja väljapüügi andmeid. Kasutati masinõppemeetodit, millele järgnes üldine lineaarne mudel (GLM) analüüsima angerjate pikaajalise asustamise ja püügi andmeid ning keskkonnaandmeid Võrtsjärve kohta, et tuvastada nendevahelisi olulisi seoseid (III).

Tulemused:

1. Peipsi pinnavee aasta keskmise temperatuuri muutus ei olnud märkimisväärne, samas leiti oluline tõus viimase kümnendi talve keskmises veetemperatuuris. Vastupidiselt oodatule ei leitud statistiliselt olulist trendi suve keskmises veetemperatuuris. Alates 2007. aastast on täheldatav märkimisväärne hiline trend jääkatte

moodustumises (ca 15 päeva), millest tuleneb pikem avavee periood. Tavaliselt hakkas esimene jää Peipsi kallastele tekkima novembri lõpus. Alates 2007. aastast on jääkate enamasti tekkinud hiljem, detsembri keskel ja selle ajaline muutlikkus on suurenenud. Järv läheb ka lahti varem, mistõttu avaveeperiood on oluliselt pikenenud. Aastaaegade lõikes täheldati juhuslikkuse suurenemist eelkõige talvistes temperatuurides. Analüüs näitas, et kliimamuutuse mõju Peipsi järve veetemperatuurile avaldub eelkõige talveperioodil (I).

2. Mudelarvutuste tulemused näitasid, et 40-60% kalade biomassi erinevustest Võrtsjärves saab seletada kirjeldavate muutujatega, mida kasutati GLS aditiivsetes ja interaktiivsetes mudelites. Kalade elupaikade ja ökoloogiliste tingimuste halvenemise indikaatorid (suur sinivetikate biomass ja nende kõrge osakaal fütoplanktonis, kõrge veetemperatuur suvel, suur toiteainete sisaldus vees) olid negatiivses korrelatsioonis kalade biomassiga. Põhjaselgrootute biomassi muutused ja teised biotilised tegurid (nt röövkalade biomass) olid samuti olulised tegurid kalade biomassi dünaamikas. Tulemused näitasid, et mõlemad, nii abiotilised kui ka biotilised tegurid mõjutavad kalade biomassi suures madalas eutroofses järves, nagu seda on Võrtsjärv (II).
3. Kõige arvukamalt esines Võrtsjärve angerjasaagis 7-aastaseid isendeid ning sel põhjusel konstrueeriti GLM mudel seitsmeaastaste intervallidega määramaks asustusaasta keskkonna (ellujäämistingimuste) mõju noorkaladele. Tuvastati nii asustusaasta kui ka konkreetse kalastusaasta keskkonnaparameetrite mõju angerjasaagile. Tulemustest ilmnes, et sinivetikate biomass ja suvine veetemperatuur klaasangerjate asustamise aastal olid suurima negatiivne mõjuga angerjasaagile 7 aastat hiljem, samas oli asustatud isendite arvu ja aerjalgsete biomassi mõju saagile positiivne. Saagikus oli positiivselt mõjutatud kalastusaasta fosfori kontsentratsioonist vees, seitse aastat varem asustatud isendite arvust ja metazooplanktoni biomassist järves. Uuringu tulemustest ilmnes, et ühtlase kalastussurve korral mõjutavad klaasangerjate asustamise aasta keskkonnaparameetrid angerjasaagi suurust rohkem, kui tingimused konkreetset kalastusaastal. Seega on klaasangerjate asustamise tingimused väga olulised angerjamajanduse edukusele Võrtsjärves (III).

Kokkuvõttes näitas töö, et kuigi talv on kliimasoojenemisest enim mõjutatud aastaaeg meie järvedes, siis uuritud kalaliikide biomass ja angerjapüük Võrtsjärves sõltusid rohkem teistest ökoloogilistest teguritest. Kuna aga talvine pinnavee temperatuur ja jääkatte teke mõjutavad kõiki keskkonnaparameetreid, ei tohi tähelepanuta jätta talvetingimuste kaudset mõju. Keskkonnamuutused võivad otseselt või kaudselt halvendada veeökosüsteemi toimimist ja kalade elupaiku, muuhulgas suurendada sinivetikate osakaalu, mille mõju kaladele võib ilmnedagi läbi mõjutatud toiduvõrgustiku osade. Erinevate tegurite mõju meie suurjärvede kaladele ja kalandusele võib ilmnedagi hilineumisega, samaaegselt mõjuvad tegurid aga üksteise toimet võimendada, mis võib viia pöördumatute tagajärgedeni.

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Parameterization of surface water temperature and long-term trends in Europe's fourth largest lake shows recent and rapid warming in winter



Burak Öglü^{a,*}, Tõnu Möls^{a,b}, Tanel Kaart^b, Fabien Cremona^a, Külli Kangur^a

^a Chair of Hydrobiology and Fishery, Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi 5, 51014, Tartu, Estonia

^b Chair of Animal Breeding and Biotechnology, Institute of Veterinary Medicine and Animal Sciences, Estonian University of Life Sciences, Kreutzwaldi 62, 51014, Tartu, Estonia

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ABSTRACT

Changes in the ice phenology, seasonal temperature and extreme events are consistent evidence of climate change effect on lakes. In this study, we analyzed multiannual variability, determined long-term trends and detected changes in the frequency of extreme events in the surface water temperature (LSWT) of Lake Peipsi (Estonia/Russia) for nearly seven decades (1950–2018) and aimed to trace how the LSWT responded to the climate change. Dynamic water temperature parameters were calculated using the smoothed water temperature curve fitted to daily water temperatures. Our results showed that, although the average LSWT did not increase significantly on an annual basis since 1950 it rose rapidly in the winter season during the last decade (-0.5°C). Ice formation exhibited a marked (-15 days) delay since 2007 resulting in a longer open water period. Extreme LSWT events did not occur more frequently. We noticed however significant fluctuating in winter LSWT in time series, starting from 2007 and also causing an increase in stochasticity. The consequences of the on-going winter warming and changes of ice cover phenology are expected to be crucial for Lake Peipsi ecosystem functioning and impact on lake biota, especially temperature-sensitive native fishes.

1. Introduction

Understanding and predicting how global warming alters the functioning of natural ecosystems is a critical challenge of the 21st century (O'Gorman et al., 2014). Lakes world-wide are impacted by climate change (Izmes'eva et al., 2016; Jeppesen et al., 2014; Jeppesen et al., 2010; Moss et al., 2011; O'Reilly et al., 2015) and can serve as sentinels for climate change monitoring, providing early indications of its effects on the ecosystem structure, function and services (Adrian et al., 2009; Lynch et al., 2016). Shallow lakes in particular quickly respond to prevailing weather conditions and are thus particularly prone to climate forcing (Wilhelm and Adrian, 2008).

Many climate change studies have focused on the analysis of water temperature dynamics in lakes, especially in large lakes (Hampton et al., 2008; Lenters, 2004). A recent global synthesis of surface summer temperature data of 235 lakes from 1985 to 2009 demonstrated that world lakes are warming quickly due to climate change, although response will vary with local conditions (O'Reilly et al., 2015). Over the study's time period about 10% of lakes cooled.

Water temperature plays a critical role in the functioning of lakes and their biota (Šporka et al., 2006). This is especially true in lakes

located at high and mid-latitude (like northern Europe) that are ice-covered in the winter period (Leppäranta, 2010; Mishra et al., 2011a; Mishra et al., 2011b). Ice cover plays an important role in lake stratification and also in heat storage which provides optimal thermal conditions for biota (Leppäranta, 2010; Mishra et al., 2011b). However, long-term warming may lead to a decrease in the ice cover period of the lake (Livingstone et al., 2010; Schindler et al., 1996). These warming trends during the winter period have been more pronounced in northern Europe and the Great Lakes of North America region in recent years (Elo et al., 1998; Livingstone and Adrian, 2009; Mishra et al., 2011b). Several studies reported an upward temperature trend in the largest lake in Europe, Lake Ladoga, especially in winter, causing a shortening of the ice cover period (Karetnikov et al., 2017; Karetnikov and Naumenko, 2011; Karetnikov and Naumenko, 2007; Naumenko et al., 2008).

Lake response can be more pronounced to extreme events than to average conditions (Nandintsetseg et al., 2007). Although lake ecosystems serve as sentinels, responding to changes in climate across the globe until recently, scientists had scant knowledge of how warming and weather extremes were affecting them (Katz et al., 2015). The intensity of the increasing non-cyclic temperature fluctuations of the lake

* Corresponding author.

E-mail address: ogluburak@gmail.com (B. Öglü).

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water influences autumn/winter warming in ice-covered lakes (Niedrist et al., 2018).

Global warming reinforces the eutrophication of already eutrophic lakes (Moss et al., 2011). Lake Peipsi (Estonia, Russia) is one of many northern large lakes showing signs of rapid change as a possible result of recent climate conditions in combination with eutrophication (Blank et al., 2009; Kangur et al., 2013; Mäemets et al., 2016). However, the most important changes were observed in the fish community: the abundance of cool-water species like vendace (*Coregonus albula* (L.)), burbot (*Lota lota* (L.)), Peipsi whitefish (*Coregonus lavaretus maraenoides*, Poljakow) and lake (dwarf) smelt (*Osmerus eperlanus morpha spirinchus* Pallas.) has declined markedly as fish community has been shifting towards more warm-water species like pikeperch (*Sander lucioperca* (L.)) and bream (*Abramis brama* (L.)) (Kangur et al., 2007). There have been several fish kills in the hot summers during heat waves and cyanobacterial blooms (Kangur et al., 2005; Kangur et al., 2013).

Despite indirect evidence for warming of surface waters of Lake Peipsi the magnitude and the seasonality of temperature change are still unknown to date. As Lake Peipsi represents alone the vast majority of the freshwater volume in Estonia, tracking variations in its thermal regime is crucial in order to assess potential impacts of climate change at the regional scale.

Here we use daily lake surface water temperature (LSWT) data collected from 1950 to 2018 to track climate change effects on Lake Peipsi LSWT, its variations and seasonality. More specifically, we aim to investigate 1) how the ice phenology has been affected, 2) if the frequency of extreme thermal events has increased, 3) if there is a higher degree of randomness in LSWT values.

2. Material and Method

2.1. Study area

LSWT data used in this study were measured in Lake Peipsi, located

south of the Gulf of Finland on the border between the Republic of Estonia and the Russian Federation. The lake (Fig. 1) is situated in the East European Plain between 7°51'–59°01' N and 26°57'–28°10' E at 30 m above the sea level. By its surface area (3,555 km²), Lake Peipsi is the fourth largest lake in Europe after Ladoga, Onego, and Vänern. The lake is shallow, with a mean depth of 7.1 m, maximum depth of 15.3 m and a volume of 25 km³. It can be divided into three basins stretching along a north-south axis: Peipsi *stricto sensu* (2611 km²), Lämmijärv (236 km²) and Pihkva (708 km²).

These figures depend greatly on the natural water level fluctuations - overall 3.04 meters over the last 80 years, with an average annual range of 1.15 m (Jaani, 2001). The average water retention time in Lake Peipsi is about two years and the water level is not regulated, causing a strong dependence of the water level on basin-scale precipitation.

Peipsi belongs to the polymictic type of lakes, where the complete mixture of water body takes place several times a year. Due to the lake's large surface area and relative shallowness, waves reach the bottom during the ice-free period. Therefore, thermal stratification is usually episodic and unstable and can be disturbed already by a moderate wind or undulation. Lake Peipsi is, as a rule, ice-covered in winter; however, ice-cover and ice-off dates have been highly variable during recent years. Furthermore, the ice cover thickness varies from year to year; the maximum thickness of ice can reach 75 cm and more. More data on Lake Peipsi is available in (Kangur et al., 2012).

2.2. Water temperature data

Daily data on LSWT in Lake Peipsi is available from 1924 and onwards. In this study we used daily surface LSWT measurements at the Mustvee hydrometric station of Lake Peipsi (58°50' N, 26°57' E) which have been in use since 1950 and is representative of Lake Peipsi s. s. open water conditions (Lieberherr and Wunderle, 2018). At the hydrometric station the surface layer LSWT in the near shore waters was measured using a Celsius mercury thermometer twice in 24 hours at 8



Fig. 1. Location of Lake Peipsi and its three basins: Lake Peipsi s.s., Lake Lämmijärv and Lake Pihkva.

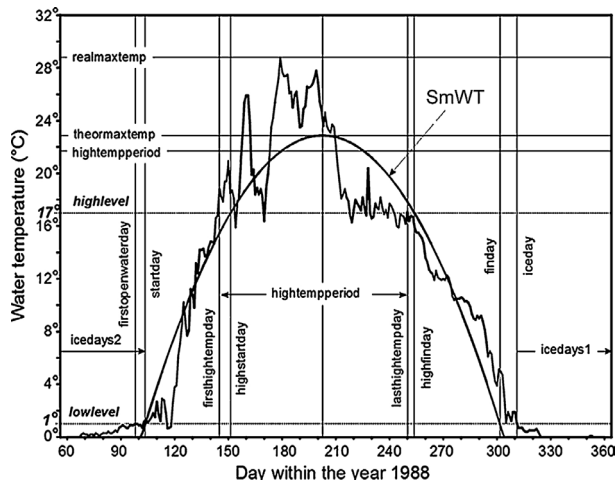


Fig. 2. Definition of selected LSWT parameters and dynamic water temperature parameters using the smoothed water temperature curve (SmWT) fitted to daily water temperatures. The pre-determined temperature parameters 'lowlevel' and 'highlevel' were set to 1 °C and 17 °C, respectively. Temperature parameters characterizing the LSWT pattern of a year are explained in Table 1.

AM and at 8 PM at a depth of 10 cm (Jaani, 2001). Since May 2009, an automatic station (VAISALA, MAWS110 and water temperature sensor QMT110) was used every hour for LSWT measurements. Daily values of LSWT in Lake Peipsi were obtained from the Institute of Meteorology and Hydrology of the Estonian Ministry of Environment and later, since 1st June 2013 from the Estonian Weather Service of the Estonian Environment Agency.

2.3. Parameterization of water temperature data

LSWT in a year is presented by various seasonal means and a specific set of constructed characteristics (duration of ice-covered period, beginning and end of ice-free period, mean for high-level temperature period, number of high-level temperature days, maximum temperature etc., Fig. 2).

In addition to raw LSWT measurements, various derived water temperature parameters were applied. The 'dynamic' LSWT parameters were deduced from the yearly LSWT fluctuation and parameters calculated by the smoothed parabola (SmWT). The two pre-determined temperature parameters 'lowlevel' and 'highlevel' were set to 1 °C and 17 °C, respectively (Fig. 2; Table 1). Both ice formation and melt-off in Lake Peipsi may last 2-3 weeks but can take up to a month. Therefore, we assumed the duration of the ice-covered period to be conventionally equal to the number of days when the temperature was < 1 °C ('lowlevel'). 17 °C was chosen due to the declining intensity of vendace feeding when the temperature rises above this threshold (Potapova, 1978). Extreme high water temperature threshold was fixed at the 97.5th percentile of temperature distribution for the whole period (23.3°C). LSWT values lower than the 50th percentile (i.e. median) were considered as "cold days" (< 5.6°C). The 'static' LSWT parameters were calculated as LSWT means for the year, for different intervals of Julian days of a year (Möls, 2005), and for four seasons: winter (December, January, February), spring (March, April, May), summer (June, July, and August), autumn (September, October, November). Temperature parameters characterizing the LSWT pattern of a year are explained in Table 1.

Table 1 Defining parameters characterizing water temperature pattern of a year. SmWT – smoothed water temperature curve by parabola from yearly water temperature (LSWT) zic-zac (Fig. 2). Pre-defined temperature parameters 'lowlevel' and 'highlevel' were set to 1 °C and 17 °C, respectively.

Parameters	Definition
Dynamic parameters	
startday	the first day when SmWT exceeded 'lowlevel' (1 °C)
firstopenwaterday	the first day when LSWT exceeded 'lowlevel'
finday	the last day when SmWT exceeded 'lowlevel'
openwater	the number of days from 'startday' to 'finday'
theormaxtempday	the day of highest SmWT value
theormaxtemp	the highest SmWT value
hightempmean	mean LSWT for days when LSWT exceeded 'highlevel' (17 °C)
realmaxtemp	the highest LSWT of a year
realmaxtempday	the day of highest LSWT value
firsthightempday	the first day when LSWT exceeded 'highlevel' (17 °C)
lasthightempday	the last day when LSWT exceeded 'highlevel' (17 °C)
hightempperiod	the period from 'firsthightempday' to 'lasthightempday'
highdays	the number of days when LSWT exceeded 'highlevel'
iceday	the last day when LSWT exceeded 'lowlevel'
epilog	from iceday to finday (epilog may be negative)
icadays1	the number of days from 'iceday' to the 31 st December
icadays2	the number of days from the 1 st January to 'startday'
icecover2	Previous year 'icadays1' + 'icadays2'
icecover	Previous year 'icadays1' + the number of days up to 'firstopenwaterday'
Static parameters	
MWT0,..., MWT7	average LSWT for eight intervals of Julian days (1-100, 100-130, 130-165, 165-200, 200-240, 240-280, 280-320, 320-365)
MWT01, MWT12, ... MWT01234567	LSWT averages for various unions of intervals corresponding to MWT0 .. MWT7
Winter LSWT	Mean LSWT of December, next year January and next year February
Spring LSWT	Mean LSWT of March, April and May
Summer LSWT	Mean LSWT of June, July and August
Autumn LSWT	Mean LSWT of September, October and November

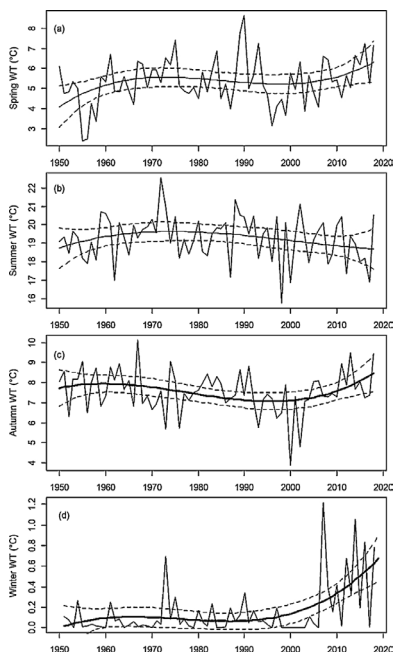


Fig. 3. Long-term mean LSWT per season (a: spring; b: summer; c: autumn; d: winter) in Lake Peipsi. Cubic regression curves predict the parameter values for different times (continuous line), the 95%-confidence limits for predictions are shown by dashed lines ($p > 0.05$, $p > 0.05$, $p < 0.05$, $p < 0.001$ for spring, summer, autumn and winter, respectively). Bold continuous lines indicate the statistically significant trend.

2.4. Statistical analysis

Statistical analyses of data were carried out using R software (R.Core.Team, 2019). To characterize the LSWT dynamics of a year, we applied descriptive statistics for different raw measurements of LSWT and various derived LSWT parameters for the periods: 1950-1972, 1973-2006 and 2007-2018. Years for intervals were selected according to result of the Wild Binary Segmentation for Multiple Change-Point Detection (WBS) on winter LSWT test by using r package 'wbs' (Baranowski and Fryzlewicz, 2019). ANOVA and t-tests were used to assess whether LSWT parameters varied as significantly across time periods. Polynomial regression analysis was applied to detect trends in LSWT parameters. 'stl' function was used for analyzing the seasonal decomposition of time series, to check randomness of the seasons and whole temperature (Cleveland et al., 1990).

3. Results

Long term selected LSWT parameters (mean water temperature, icecover, finday and epilog) and seasonal temperature trends are given in Figs. 3 and 4. All the other parameters in three intervals (1950-1972, 1973-2006, 2007-2018) were included into Supplementary Table A.1.

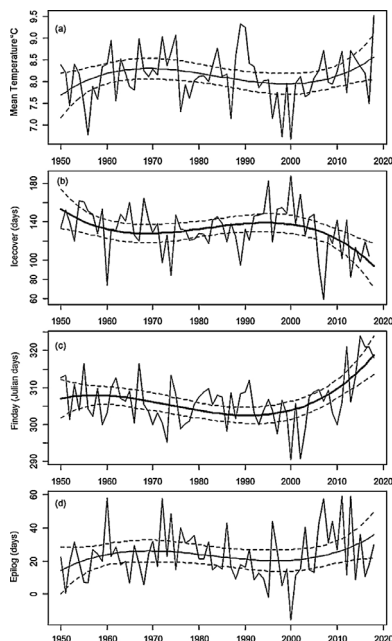


Fig. 4. Long-term changes of selected parameters in Lake Peipsi. Cubic regression curves predict the parameter values for different times (continuous line), the 95%-confidence limits for predictions are shown by dashed lines. Annual mean LSWT (a) is annual average LSWT, icecover (b) denote the annual length of the ice-covered period (calculated from LSWT), Finday (c) represents the Julian day of SmWT lower than 1°C and Epilog (d) represents the days between starting of ice and permanent ice cover (LSWT-SmWT). ($p > 0.05$, $p < 0.001$, $p < 0.001$, $p > 0.05$ for Mean water temperature, Icecover, Finday, Epilog, respectively). Bold continuous lines indicate the statistically significant trends.

Although spring and summer LSWT showed an upward and downward trend respectively, they were not statistically significant. However, strong, significant water temperature changes occurred in winter and autumn. Fig. 3a and c panels reveal that there were only marginal changes in temperature from the start of the measurements (1950) to the early 1990's in all seasons but autumn as the trend of the 1950-1970 period was mirrored in 1970-1990. Starting that time, LSWT rose for all seasons but summer (which exhibited a slight decline). LSWT rise has been especially dramatic in winter, jumping from 0.15 °C in 2000 to 0.63 °C nowadays. The record high winter LSWT was attained in 2007 with an average 1.2 °C. Fluctuation of the LSWT in years had been increasing again from 2007 in winter.

Although seasonal trends in LSWT were significant for autumn and winter, this did not translate into the annual average as the yearly LSWT trend was not significant. The Fig. 5 shows that the warming of Peipsi in winter did not correspond to a decrease in the number of cold-water days ($T < 5.6$ °C). However, a significant trend was detected on the ice phenology (Fig. 4b). From 1950 to 2018, ice formation in Lake Peipsi has been delayed by two weeks on average. At the same time

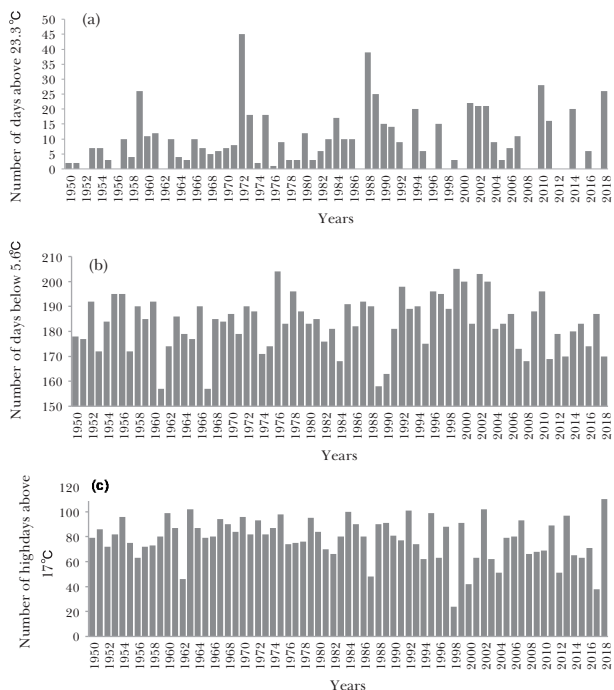


Fig. 5. Bar plot of days below and above selected thresholds of LSWT in Lake Peipsi. Threshold calculated as above 97.5th (a), and below 5th (b) quantiles of the LSWT dataset. (c) corresponds to the LSWT 17 °C.

total ice cover duration dramatically decreased. Trend of the epilim was not significant, however comparison of the three intervals showed an increase in days of permanent ice during the 2007–2018 period (Supplementary Table A.1).

No significant trend was observed in the frequency of hot or very hot LSWT events (Fig. 5). However, among the five years during which occurred the highest number of very hot LSWT (> 23.3°C) days (1959, 1972, 1988, 2010 and 2018) two were from this century. The trend for cold LSWT days which were represented by days below 5.6°C was not significant. The lowest count of cold LSWT days were found in 1961 and 1967 with 157 days whereas the highest number of days when LSWT was exceeding 17 °C was found in 2018 (Fig. 5c). However, the 2000s and 2010s did not differ in that regard with the 20th century.

Seasonal decomposition of time series in spring, summer, autumn and whole year LSWT were given in Supplementary material (Figs. A.1–A.4). The decomposed time series of winter LSWT shows that there is a visible increase in the variance of winter LSWT which started in 2007 and that is displayed in both trend and randomness components (Fig. 6).

Intervals for three periods (1950–1972, 1973–2006, 2007–2018) are given in Supplementary Table A.1. Most of the significant changes occurred in the last period. The following parameters finday, openwater, iceday, epilog, icedays1-2, icecover1-2, MWT0, MWT7, winter LSWT,

openwater temperature, MWT07 and firstopenwaterday were found significantly different between the periods. Winter related parameters (temperature, ice phenology, days of ice, open water days) were indicating the changes in winter. Changes in permanent ice formation (iceday) were not significant during the first two periods (1950–1972 and 1973–2006), however a dramatic shift occurred during the last one. In the last period of the study (2007–2018), ~15-days delay was observed in permanent ice cover formation, compared to the average permanent ice formation during the whole study period (1950–2018). The LSWT of the last 45 days of the year (MWT7) increased in the last period (2007–2018). It was approximately two times higher than in the average of whole periods (1950–2018) and reached an average 1.25 °C.

Epilog was investigated to identify the duration of ice formation process to reach a permanent ice cover. Fig. 4 reveals that there has been a slight delay in the number of days of permanent ice forming in the last decade.

4. Discussion

The present study emphasizes that several temperature-related parameters were investigated to evaluate how Peipsi responded to climate change from the mid-20th century to nowadays. Most of the changes relative to the 1950's occurred in the 1990's and from 2007

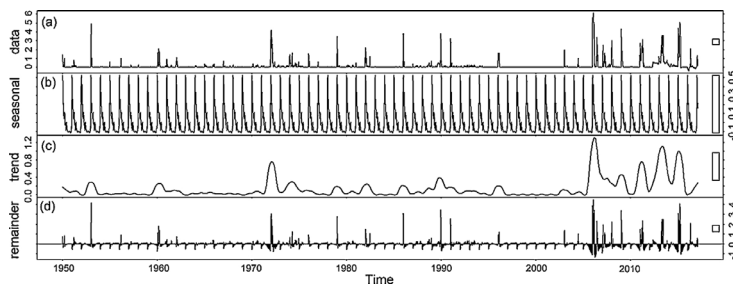


Fig. 6. Seasonal decomposition of time series in winter LSWT. (a): data, (b): seasonal component, (c): trend component, (d): random component. The daily observed data (winter) for 69 years (a), seasonal effect was given in panel (b), the panel (c) indicating trend of the data and remainder of those three components was given in the panel (d). The remainder/noise were calculated as the residuals from the seasonal and trend fit. Remainder indicates the randomness of the data in time series that tend to increase from year 2007. Relative comparison of the magnitudes of each component is given right side of each graph as bar.

onwards. Our results revealed that winter-related LSWT parameters were the most affected by climate change in Lake Peipsi.

Our study in Lake Võrtsjärv, which is the second largest Estonian lake showed a significant annual temperature increase in the last 40 years (Cremona et al., 2018). An increasing water temperature trend was captured in Lake Peipsi and Lake Võrtsjärv dates between 1940–2011 (Nöges and Nöges, 2014). Despite, the size difference between Võrtsjärv and Peipsi, the yearly average water temperature was not significantly different. However, ice formed later and disappeared earlier on Peipsi (Nöges and Nöges, 2014). In our study, the annual mean LSWT showed a slight rise in the last decades that was not significant. The lake temperature increases in two central Europe lakes (Wörthersee/Austria and Mondsee/Austria) were in the last 30 years during the study period 1910–2016 (Woolway et al., 2017). It has been predicted a rise of 3 °C in Austrian large lake water column for 2050 (Dokulil, 2014). Other study shows that the average rate of summer LSWT increases in lakes (0.34 °C per decade) between 1985 and 2009 have been even faster than annual average increase in air temperatures (0.25 °C per decade) (O'Reilly et al., 2015) and 0.12 °C per decade increase on ocean surface temperatures over a similar period (1979–2012) (Hartmann et al., 2013). However, warming of lakes around the globe is highly variable and lake warming rates were heterogeneous even within regions (O'Reilly et al., 2015). Large heterogeneity in lake summer surface LSWT trends is associated with diverse climate and geomorphic factors (O'Reilly et al., 2015).

Shallow lakes (e.g., like Peipsi) and their ectothermic biota are particularly vulnerable to the effects of climatic warming (Moran et al., 2010). One of the most striking outcomes of this study was a recent and rapid rise in winter temperature which started in 2007. Lake Ladoga, which is Europe's largest lake and located in a close geographical area has also exhibited a warming trend in 2007 compared to the previous 65 years (Karetnikov and Naumenko, 2011). Similarly, Carvalho and Kirika (2003) reported that a marked upward trend in water temperature was observed in winter and spring months in Loch Leven. Similar results were found in Urmia Lake Basin (Iran) that changes in temperature were mostly visible in winter and spring although this lake does not ice cover (Deju et al., 2013). Average winter and early spring lake water temperature are increasing in two shallow lakes (Müggelsee and Heiligensee) in Germany, with a projected stronger temperature rise in winter (Kirillin, 2010). The author predicted also changes in the mixing regime of the lakes, with a gradual switch from polymictic to warm monomictic by 2100 (Kirillin, 2010). One of the opposite results to compare with our study is a trend of increasing water temperature in summer and decreased in winter in one sampling point of Finnish Lake

Pyhäselkä (Voutilainen et al., 2014). The authors commented that the most likely causal factor were wind-induced water currents in the lake (Voutilainen et al., 2014). Parameters such as depth, volume, the surface area of the lake, and Secchi depth can carry great importance for ice phenology and surface water temperature of the lake (Bernhardt et al., 2012; Ptak et al., 2018a). Bernhardt et al. (2012) reported that deeper and clearer lakes have shorter ice duration than shallow and less clear lakes.

Several studies confirmed that air temperature in winter in the northern hemisphere is controlled by North Atlantic Oscillation (NAO) (Hurrell, 1995; Jennings et al., 2000; Wrzesiński et al., 2015; Wrzesiński et al., 2018). Changes in NAO have strong, large scale effects on local temperature (George et al., 2004; Ptak et al., 2018b). Jaagus and Kull (2011) commented that increasing winter air temperature in Estonia is associated with NAO through wind direction and intensity. The strongest correlations between NAO and lake water temperature in Polish lakes were detected in December, January, February and March in particular (Ptak et al., 2018b). Changes in the winter LSWT and ice phenology in the case of Lake Peipsi might be the consequences of NAO as well. Additionally, as Peipsi is located in the transition zone between maritime and continental climate this can play an important role for the significant shift in the winter dynamics (atmospheric and lake winter parameters like temperature, snowfall, ice) (George et al., 2004; Sepp et al., 2018).

We did not observe changes in the frequency of hot or very hot LSWT events during the study period which is at odds with the expected outcomes of global warming. Benson et al. (2012) indicated that significant increases in frequency of extreme in warmer conditions while decreases in the frequency of extreme events were associated with cooler conditions in 75 different lakes. A study in Hövsgöl Basin area (Mongolia) showed a parallel increase in hot days and decrease in cold days (Nandintsetseg et al., 2007). Not only the occurrence of higher temperature events but also the duration of warmer periods must be taken into account as it is important for the growth rate of many organisms (Schindler et al., 1996) and although the frequency of extreme events did not increase during the last decades, small incremental rise in LSWT might bring serious consequences for cold stenothermic species.

Ice cover is a sensitive indicator of global climate and changes in ice cover can explain well the local climate conditions (Brown and Duguay, 2010; Cheng et al., 2014; Karetnikov and Naumenko, 2007). Many studies recorded that ice cover period is delaying or shortening in lakes located in the boreal region (Couture et al., 2015; Korhonen, 2006; Leppörranta et al., 2019). Our findings show that open water days (ice-

off) increased during the study period. Similar result was reported in Morskie Oko Lake (Poland), where ice cover duration decreased between 1971 and 2007 and continuous ice cover period strongly decreased in the period of 1996-2007 (Ice formation started 1.2 days per decade later, ice melting 4.1 days per decade earlier) (Choiński et al., 2010). A 50 year (1961-2010) observation on 18 Polish lakes ice phenology showed that average ice cover shortened because of a delay in the ice forming (2.3 days per decade) and an earlier melting (5.6 days per decade) (Choiński et al., 2015). Authors pointed that individual lakes show discrepancies in ice phenology within the same regions, because of regional atmospheric circulation (Choiński et al., 2015). A study of Latvian lakes showed that ice cover periods tended to decrease as well as the surface water temperature increases in most of the lakes during the study period 1945-2002 (Apsite et al., 2014). The result of the long-term monitoring (1955-2017) shows that ice cover duration of the two largest lakes in Europe (Lakes Onego and Ladoga) is around 20 days shorter because of a delay in the ice formation (Filatov et al., 2019). A study conducted in Antarctic lakes showed that permanent ice cover of Signy Island has receded by 45% since 1951 and 63 days open water period increased by the rise of 0.5°C summer temperature (Quayle et al., 2002). As Peipsi is not stratified, changes in water temperature are not restricted to the epilimnetic part of water column (Moran et al., 2010; Prowse et al., 2011). Since the duration of the ice cover depends directly on winter air temperature (Jackson et al., 2007) a rise in temperature in that season can lead up to 15 days more of open water as shown for boreal lakes in north-western Ontario in Canada (Schindler et al., 1996). Previous study in Peipsi confirmed that the ice formation and break off reflects well the changes in air temperature (Nöges and Nöges, 2014) and rise in winter air temperature during study period 1756-2014 in Estonia was observed while changes in summer air temperature were insignificant (Eensaar, 2016, 2019).

Strong annual fluctuations in LSWT were detected in the 2007-2018 period but only during the winter season in Lake Peipsi. Atmospheric variability in the northern hemisphere is influenced by the NAO factor and winter variable (including wind and ice cover) fluctuations are dependent of NAO in northern Europe (Janssen et al., 2004; Omstedt and Chen, 2001; Yoo and D'Odorico, 2002). Hurrell et al. (2003) indicated that fluctuations of the NAO are largely unpredictable between months and even years. The winter LSWT amplitude varied between 0.01-1.2 °C in period 2007-2018 which is twice greater than for the other periods. Besides the average warming in winter time, this greater temperature fluctuations might cause an increase in the unpredictability of ice cover during this season as consistent negative temperatures are needed for consolidating the ice (Nandintsetseg et al., 2007; Niedrist et al., 2018). Ice cover interruption by the fluctuations might fragilize the ice and thus be hazardous for human activities relying on ice cover.

5. Conclusion

We have shown that although annual mean LSWT did not change significantly during the last seventy years winter LSWT increased rapidly and dramatically during the last decade, causing a rapid shortening of the ice cover period. On average, the open water period is now longer than at the beginning of the century. These changes in ice phenology were accompanied by a greater unpredictability of winter temperatures, causing a threat on ice cover stability. Besides the important consequences on lake functioning (water column stability, thermal exchange, dissolved gas concentrations) a weaker ice cover is also susceptible to affect ecosystem service provisioning (ice fishing, ice roads) for local populations.

CRedit authorship contribution statement

Burak Ögüü: Conceptualization, Methodology, Software, Formal analysis, Writing - original draft, Writing - review & editing,

Visualization. **Tõnu Möls:** Methodology, Software, Formal analysis. **Tanel Kaart:** Methodology, Software, Formal analysis, Writing - review & editing, Data curation. **Fabien Cremona:** Conceptualization, Methodology, Writing - original draft, Writing - review & editing, Data curation, Supervision. **Küllü Kangur:** Supervision, Resources, Data curation, Writing - review & editing, Writing - original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.limno.2020.125777>.

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Is fish biomass controlled by abiotic or biotic factors? Results of long-term monitoring in a large eutrophic lake

Burak Öglü*, Upendra Bhele, Ain Järvalt, Lea Tuvikene, Henn Timm, Siim Seller, Juta Haberman, Helen Agasild, Peeter Nöges, Maidu Silm, Priit Bernotas, Tiina Nöges, Fabien Cremona

Chair of Hydrobiology and Fishery, Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi 5, 51006 Tartu, Estonia

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ABSTRACT

Relationships between biomass and ecological factors including trophic interactions were examined to understand the dynamics of six fish species in Lake Võrtsjärv, a large shallow eutrophic lake located in Estonia (north-eastern Europe). The database contained initially 31 predictive variables that were monitored in situ for nearly forty years. The strongest predictive variables were selected by three parallel approaches: single correlation (Pearson), a multivariate method (Co-inertia analyses), and a machine learning algorithm (Random Forests), followed by a Generalized Least Squares model to determine meaningful relationships with fish biomass. Models with both additive and interactive effects were constructed. The results revealed that the indicators of degraded ecological conditions (high cyanobacteria biomass and their proportion in total phytoplankton, high summer temperature, high nutrient concentration) were negatively correlated to fish biomass. Benthic macroinvertebrates and other biotic predictors (biomass of specific fish prey and predators) were also important contributors to fish biomass dynamics. Together, abiotic and biotic factors explained 40–60% of the variance of fish biomass, depending of the species. Our findings suggest that both abiotic and biotic factors control fish biomass changes in this eutrophic lake.

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Introduction

Inland aquatic systems bear a great importance for the conservation of local and global biodiversity, as they harbour 40% of global fish species, while covering <2% of the Earth's surface versus 71% for oceans (Lundberg et al., 2000; Moss, 2000; Wetzel, 2001). Most of the world lakes are shallow and exhibit high taxonomic richness and productivity (Meerhoff and Jeppesen, 2009). Numerous shallow lake catchments are located in lowland areas inhabited by people for thousands of years (Cheng et al., 2010) and thus have been chronically impacted by human activities. More recently, enhanced eutrophication and ongoing global climate change has further degraded the ecological status of shallow lakes (Moss et al., 2011; Willemssen, 1980) and caused also a lack of proper food supply and low reproductive success of fish (Willemssen, 1980). Global warming can affect fish directly as they are lacking physiological thermoregulation and indirectly through biotic interactions, changes in O₂ concentrations, and modification of habitat (Jeppesen et al., 2010). Due to different adaptation mechanisms, the responses of fish populations to climate change could vary largely (Rijnsdorp et al., 2009). Strong changes in the fish community structure of large and

shallow lakes Võrtsjärv and Peipsi during the last decades have been attributed to the alteration of nutrient loading and consequent eutrophication pressure as well as to changes of local climate (Kangur et al., 2002).

Understanding of the joint effect of different abiotic factors on fish community structure would help to diagnose and predict the ecological dynamics of lake ecosystems (Beisner et al., 2006; Cheng et al., 2010). According to Jackson et al. (2001), the relative importance of biotic versus abiotic factors to fish communities depends on the spatial scale of the case study, with biotic factors being more important in small-scale than in large-scale studies. In addition, the responses to extreme events can depend on the body size of fish species (Jackson et al., 2001; Kangur et al., 2016). Biotic relations are critically important for the community structuring, especially in shallow lakes where the top-down regulation of productivity and biota by trophic cascades often predominates over bottom-up nutrient control (Jeppesen et al., 2010; Kangur et al., 2002; Lemmens et al., 2018; Olin et al., 2006; Williams and Moss, 2003).

Håkanson and Gyllenhammar (2005) highlighted that some single stressors such as extensive fishing, eutrophication, toxic contamination or other abiotic factors cannot sufficiently explain the complex interactions in multi-stressor systems. To understand such systems, several studies have applied models that can evaluate the

* Corresponding author.

E-mail address: ogluburak@gmail.com (B. Öglü).

interactions between multiple biotic and abiotic variables with multivariate approaches (Bianchi and Høisæter, 1992; Cremona et al., 2018b; Gebrekiros, 2016; Leathwick et al., 2006; Trigal and Degerman, 2015). Machine-learning algorithms, in particular, are useful for selecting the most meaningful variables among a large set of predictors (Breiman, 2001; Feld et al., 2016; Trigal and Degerman, 2015) – a task that otherwise would be very tedious.

Our aim in the present study was to analyse which ecological factors, including biotic (interspecific) relationships and abiotic (environmental) variables are mainly controlling the dynamics of fish community structure in Lake Võrtsjärv, a large and eutrophic shallow lake located in Estonia. Following Jackson et al. (2001), our main working hypothesis was that abiotic variables were better predictors of fish species biomass than biotic variables considering Võrtsjärv as a large system.

Material methods

Study area

Lake Võrtsjärv is situated in central Estonia (58°05'–58°25' N and 25°55'–26°10' E), in the southern boreal (or hemiboreal) forest zone. With a surface area of 270 km², it is the second largest lake of the country. Võrtsjärv is a shallow lake with a maximum depth of 6 m and average depth of 2.8 m. The long-term average annual ice cover duration is 135 days, and the lake is mostly turbid (Secchi depth < 1 m) during the ice-free period owing to frequent sediment resuspension (Cremona et al., 2017). Average annual water level fluctuation is 1.4 m and absolute water level fluctuation interval 3.2 m (Järvet et al., 2004). The lake is eutrophic and the dominant primary producers are cyanobacteria representing 60–95% of the total phytoplankton biomass (Cremona et al., 2014). The average concentration of total phosphorus (TP) in the lake is 48 µg l⁻¹, that of total nitrogen (TN) 0.91 mg l⁻¹, and chlorophyll *a* (Chl *a*) 36 µg l⁻¹ (Nöges et al., 2008). The ratio of TN to TP (TN/TP in following text) was also calculated based on weight units. Six ecologically and economically important fish species have been selected for this study: pike, *Esox lucius* L.; perch, *Perca fluviatilis* L.; pikeperch *Sander lucioperca* (L.); ruffe, *Gymnocephalus cernuus* (L.); bream, *Abramis brama* (L.); white bream, *Blicca bjoerkna* (L.). Most species are not subjected to a strong fishing pressure with the exception of pike. During the 1979–2016 period, 22% of total pike biomass, but only 8% of total perch, 3% of total pikeperch and 3% of total bream were caught by commercial fishing (Cremona et al., 2018a).

Data collection and examination

Water samples for chemical and plankton analysis and sediment samples for macroinvertebrate analysis were collected on a monthly basis (biweekly or weekly for some shorter periods) between 1979 and 2016. Water temperature was measured by the Estonian Institute of Hydrology and Meteorology (presently Estonian Environment Agency) according to the protocol of guidelines by World Meteorological Organization (Nöges et al., 2010; WMO, 1994, 2008). Seasonal mean water surface temperatures were calculated for 3-month-long seasons starting winter from December 1.

Water-column integrated samples for chemical components, phyto- and zooplankton were taken with Ruttner sampler from the pelagic monitoring station situated in the deepest area (around 6 m) of the lake. This sampling site is representative of >90% of the lake area (Nöges and Tuvikene, 2012). Analyses of water chemistry (TN, TP, PO₄, NO₃, HCO₃) were performed at the Tartu laboratory of the Estonian Environmental Research Centre according to the international (ISO) and Estonian (EVS-EN ISO) quality standards. Concentration of dissolved oxygen (O₂) was measured using portable electrochemical oxygen meter, and water transparency with Secchi disk. Water level

was measured by the Estonian Weather Service at the outflow of Võrtsjärv with the reference point being the altitude of 33.01 m.

Ten litres of the depth-integrated water was filtered through 48-µm mesh size plankton net to get samples for zooplankton (Zingel et al., 2019). Both phytoplankton and zooplankton were preserved with acidified Lugol's iodine (0.5% final concentration). The biomass of phytoplankton was measured with Utermöhl (1958) method, using inverted microscope at 600× magnification. Zooplankton was counted under binocular microscope (×32–56 magnification) and the average body length of at least 20 individuals of each taxon was measured for biomass calculation (Agasild et al., 2007).

Macroinvertebrate (BMI) samples were collected during the ice-free period using two Ekman-type grabs; Borutski sampler (box height 40 cm) in the profundal and Zabolotskij sampler (box height 20 cm) in the littoral zone. The invertebrates were sampled alive, treated with 70% alcohol and then weighted after drying (Kangur et al., 1998).

Fish was caught in daytime during the ice-free period (April–November, 15–20 hauls per year) with bottom otter trawl (mesh size 12 mm at cod end). Trawling was done for 15–30 min at the speed of 4.5 km h⁻¹. The width of the trawl was 8 m and the height 2.5 m. One hour of trawling was equal to 5 ha of lake surface. WPUE (weight per unit effort) catchability and fishing effort were used to calculate the biomass proxy ($B = q^2 C/F$) (Nöges et al., 2016).

An initial set of 25 descriptive and ecologically relevant variables ("predictors") were selected. The abiotic variables consisted of nutrients and physical characteristics whereas biotic variables were the biomasses of fish species and other food web components. A complete list of variables is provided in the Electronic Supplementary Material (ESM) Table S1. All data were averaged to yearly values for reducing seasonal effect.

Data analysis

Statistical analyses of data were carried out using R project 3.4.3 and SPSS 20.0 statistical package program (IBM SPSS, 2011; R Core Team, 2017).

Data transformation

Shapiro-Wilk test was run for analysing normality of the data and residuals. Log-transformation was applied to parameters which had shown non-normal distribution in order to reduce model heteroscedasticity and to improve their conformance to linear regression.

Variable selection

Considering the large number of predictive variables and their possible interactions, we decided to employ three different, parallel statistical approaches for selecting the most sensible ones. At all stages of the analyses, we also considered the ecological relevance of predictors in order to avoid selecting those that show only mechanistic relationships with variables.

We first aimed at selecting the most influential predictors for fish community biomass. For detecting collinearity between variables, the Variance Inflation Factor (VIF) method was used first (R package *usdm*) with the VIF threshold set at 8 (Cremona et al., 2018b; Feld et al., 2016; Naimi, 2015; Zuur et al., 2007). Variables that exceeded the threshold value were excluded from further analysis and the three statistical approaches run on the rest for determining the most influential ones.

To assess the statistical associations between parameters, Pearson correlation analysis was applied on the whole dataset and the R package *corrplot* used to illustrate the correlation coefficients (Wei and Simko, 2013). Secondly, a co-inertia analysis (COI) (Dray et al., 2003) was carried out to discover common patterns among fish biomass and other

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factors, based on principal component analyses (PCA) (Chessel et al., 2004). The overall concordance, measuring the correlation between tables of biomass and factors, was estimated in the form of the RV-coefficient, followed by the permutation test for statistical significance. The COI was performed with the R package *ade4* (Dray et al., 2007). Finally, a Random Forests (RF) test was performed to select suitable parameters and most effective and meaningful interactions for each fish species biomass in the model (Ishwaran and Kogalur, 2017).

Model construction

Generalized Least Squares (GLS) test was applied to the three best predictors of each fish biomass estimate (Table 1) by using the R package *nlme* (Pinheiro et al., 2007). We tested both additive and interaction effects. The residual autocorrelation function 'AFC' test measuring the strength of the dependency between time points, was applied to the models (Crawley, 2013; Cremona et al., 2018b). ACF values lower than 1 within a 95% confidence interval indicated the absence of significant temporal correlation within data whereas values >1 denoted some degree of temporal autocorrelation that should be modelled. In the present study, no significant temporal autocorrelation was detected. We nevertheless applied a first order autoregressive factor (AR1) to check whether it resulted in an improvement of the model. Akaike's Information Criterion AIC (Akaike, 1973) was used for evaluating the model performance. We applied 'dredge' function for automated model selection through AIC values of the models by using the *MuMIn* package in R (Barton, 2018). Within the delta AIC (Δ AIC) range of 2, the models compared were considered equally supported (Anderson and Burnham, 2004) and the best model was selected taking into account the simplicity and parsimony (lower degree of freedom).

Results

Temporal changes in fish biomass

Fish biomass declined from the late 1970's and reached a minimum in the early 2000's (Fig. 1). After that the biomass rose again, exceeding recently the late 20th century values for white bream and bream (R^2 0.59, and 0.51, respectively, $p < 0.001$). There were significant negative trends in the biomass of pikeperch and pike (R^2 0.56 and 0.35, respectively, $p < 0.001$) which never regained the same biomass as in the early 80's whereas there was no significant change for perch and ruffe (R^2 0.12 and 0.15, respectively, $p > 0.05$).

Importance of predictive variables

Omitting mechanistically related variables (like total fish biomass and specific biomasses, phytoplankton and cyanobacteria biomass, etc.), the strongest correlation was found between white bream biomass (onwards for brevity reasons the specific biomasses are denoted by the species names only) and HCO_3^- ($r = 0.64$, $p < 0.001$, Fig. 2). Significant correlations for pike were pikeperch ($r = 0.37$, $p < 0.001$), perch ($r = 0.46$, $p < 0.001$) and summer temperature ($r = -0.31$, $p < 0.05$). Pikeperch correlated with bream ($r = 0.37$, $p < 0.05$), summer temperature ($r = 0.33$, $p < 0.05$), water level ($r = 0.32$, $p < 0.05$), phytoplankton ($r = -0.45$, $p < 0.001$), cyanobacteria ($r = -0.51$, $p < 0.001$) and the proportion of cyanobacteria in phytoplankton (cyan/phy) ($r = -0.42$, $p < 0.001$). Bream correlated with white bream ($r = 0.42$, $p < 0.001$), ruffe ($r = 0.40$, $p < 0.05$), benthic macroinvertebrates ($r = 0.36$, $p < 0.05$), summer temperature ($r = -0.42$, $p < 0.001$) and cyan/phy ($r = -0.40$, $p < 0.05$). White bream correlated with perch ($r = 0.41$, $p < 0.001$) and ruffe ($r = 0.36$, $p < 0.05$). Perch correlated with ruffe ($r = 0.58$, $p < 0.001$) and ruffe with benthic macroinvertebrates ($r = 0.40$, $p < 0.05$).

All variables in the dataset were divided into five clusters among which temperature-related variables grouped with nutrients, O_2 and phytoplankton composition into one and fish species with alkalinity, NO_3^- , and water level into another clusters (Fig. 2). Rather strong negative correlation was observed between total fish biomass (representing the sum of the six species) and cyan/phy ($p < 0.001$, $r = -0.42$, Fig. 3).

The co-inertia analysis (COI) revealed a statistically significant relationship between abiotic variables and biomass of fish ($p < 0.001$) as the RV-coefficient, an index of strength of the relationship, was 0.34 (Fig. 4). The first two axes of the COI accounted for 60.6% and 14.9% of the explained variance, respectively. The weights of initial variables in common patterns indicated that the higher temperature values (summer, autumn and yearly mean) corresponded to the years with more phytoplankton and cyanobacteria, and with less rotifers, pike and pikeperch. The higher TN/TP and winter water temperatures were negatively related with biomasses of white bream, ruffe, perch, benthic macroinvertebrates, and bream. HCO_3^- was strongly positively related with white bream. As indicated in Fig. 4C, consecutive numbers grouped together signified that variable values clustered by year of sampling. NO_3^- was the least significant among the abiotic factors.

On the variable importance plot of the random forest (RF) test, each graph represents the ranking of predictor variable importance for single fish species biomass (Fig. 5). The RF results show that for all fish species, except perch, there was at least one abiotic variable among the first five most important predictors. For pike, pikeperch and ruffe, two parameters out of five were abiotic. Nutrient-related parameters were important only for top predators while cyanobacteria and temperature-related parameters were found important for most fish species. The three most important variables for explaining pike biomass variance were perch, NO_3^- , and pikeperch. For pikeperch they were bream, TN/TP and NO_3^- ; for bream – white bream, summer temperature and cyan/phy; for white bream – HCO_3^- , bream and perch. For perch and ruffe, the three most important variables were all the biomasses of other fish species: ruffe, pike, and white bream for perch; perch, bream and white bream for ruffe. Although, according to RF analysis, NO_3^- appeared as one of the most important variables for explaining the variance of pike, we did not use it in the GLS model because of low and insignificant weight in COI.

Model performance and explanatory power

GLS model was run for each fish species with the pre-selected predictive variables as given in Table 1. Models that were constructed without autoregressive factors AR1, provided better AIC values while satisfying model assumptions regarding temporal autocorrelation (ESM Table S2). Hence, all GLS models were applied without AR1. The model outcome revealed that 40% to 60% of the variance of fish biomasses could be explained by the descriptive variables that were used in the GLS models (Fig. 6). Temperature-related parameters were used in three models. In addition, benthic macroinvertebrates were used in three models due to their ecological importance as well as correlations and COI results. For pikeperch and bream, predictors with additive effects were used to explain their biomass. However, models with interactive effects obtained the best AIC values for white bream and perch. For ruffe and pike, a combination of interactive and additive effects performed best. Summer temperature (-), perch (-) and benthic macroinvertebrates (+) explained 45% of pike biomass (Table 1, Mod1). Mod2 showed that 43% of the variance of pikeperch biomass was explained by cyanobacteria (-), TN/TP (+) and bream (+). Mod3 explained 40% of bream biomass with benthic macroinvertebrates (+), summer temperature (-) and pikeperch (+). Perch had the highest variance (60%) (Mod5) whereas it was only 41% for ruffe. For white bream, HCO_3^- and perch had a positive and rotifers a negative impact.

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Table 1
Generalized Least Squares models with selected descriptive variables (number of observations n = 38).

Model Number	Response variables	Descriptive variables	Model	AIC	df
Mod1	Pike biomass (B_{Pike})	Summer temperature, Perch, BMI	$\log(B_{Pike}) = \log(B_{BMI}) + \log(B_{Perch}) + \log(\text{summer temperature})$	75.4	7
Mod2	Pikeperch biomass ($B_{Pikeperch}$)	TN/TP, Bream, Cyanobacteria	$\log(B_{Pikeperch} + 1) = \log(\text{TN/TP}) + \log(B_{Bream}) + \log(B_{Cyanobacteria})$	51.4	5
Mod3	Bream biomass (B_{Bream})	Pikeperch, Summer temperature, BMI	$\log(B_{Bream}) = \log(B_{Pikeperch}) + \log(\text{summer temperature}) + \log(B_{BMI})$	26.1	5
Mod4	White bream biomass (B_{Wbream})	HCO_3^- , Rotifer, Perch	$\log(B_{Wbream}) = \log(\text{HCO}_3^-) + \log(B_{Rotifer}) + \log(B_{Perch})$	99.7	9
Mod5	Perch biomass (B_{Perch})	Ruffe, Cyan/phy, White bream	$\log(B_{Perch}) = \log(B_{Ruffe}) + \log(\text{cyan/phy}) + \log(B_{White\ bream})$	84.1	9
Mod6	Ruffe biomass (B_{Ruffe})	BMI, Spring temperature, HCO_3^-	$\log(B_{Ruffe}) = (\log(B_{BMI}) + \text{spring temperature}) + \log(\text{HCO}_3^-)$	107.6	7

Discussion

Our results highlighted linkages between the long-term dynamics of fish community biomasses and ecological variables. The GLS analysis showed that 40% to 60% of the variance of different fish species biomasses could be explained by co-interacting abiotic and biotic factors. The RF analysis highlighted that the top three predictors for fish biomasses (with the exception of ruffe and perch) comprised at least one abiotic variable. Nutrient-related predictors were especially important for the two piscivorous species, pike and pikeperch, while alkalinity was strongly related to white bream biomass.

Outcomes of the RF test showed that most effective predictors for ruffe were other species biomasses (perch and bream mainly) and

spring water temperature. The appearance of other fish species among the top predictors of particular fish species biomass can be explained by (i) trophic (i.e. prey-predator) relationships, (ii) interspecific competition, or (iii) dynamic congruence. For ruffe, the strong relationships were likely due to food competition with bream for low chironomid larvae biomass in summer (Kangur et al., 2004). McLean (1993) indicated that ruffe is able to adapt to a wide range of habitats and shows high reproductive activity. Therefore, its biomass seems to depend more on interspecific relationships than on other ecological factors. The positive spring temperature effect on ruffe biomass might be caused by favourable spawning conditions during warm springs (Brown et al., 1998). The interaction with benthic macroinvertebrates was an expected predictor for ruffe (Mod6) as soft-bodied macroinvertebrates

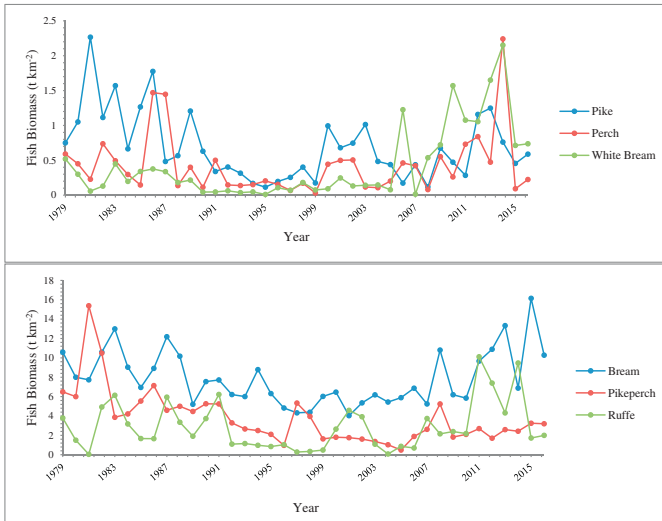


Fig. 1. Time series of fish biomasses of six species. For clarity purposes, species within similar biomass ranges are grouped separately.

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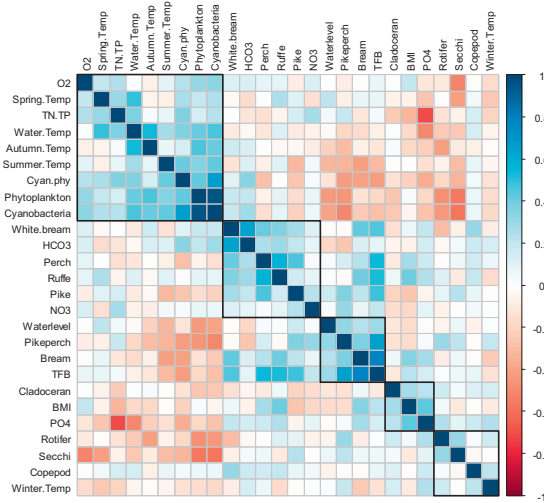


Fig. 2. Pearson correlation between the fish biomasses and ecological variables. Colour of the boxes indicates the relationships of the variables based on correlation coefficients. Blue shades show positive correlations while red shades represent negative correlations. The intensity of the shade and the size of the tiles indicate the strength of the correlation. Variables are ordered according to the hierarchical clustering and darker square frames indicate proximity in group of variables. BMI: benthic macroinvertebrates, TFB: total fish biomass. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

are among its favourite prey items (Fullerton et al., 1998; Ogle et al., 2004). Ruffe is often presented as an undesirable fish that preys on other species eggs and larvae (McLean, 1993; Raloff, 1992) and as an invasive species in lakes of North America where it competes for food with yellow perch, trout-perch, and other native benthivorous fishes (Fullerton et al., 1998; Ogle et al., 1995; Savino and Kolar, 1996). However, ruffe is a native species in most of the north, central and eastern European lakes including Vörtsjärvi (Simon and Vondruska, 1991). The modelled positive association between ruffe and perch might be caused by a dynamic congruence caused by common positive or negative

abiotic factors that remain to be investigated. Ruffe is a food resource for pike, and the high abundance of ruffe might weaken the predator pressure on perch (Kangur et al., 2004).

The biomass of perch was also strongly correlated with biomasses of other fish species. Perch can tolerate poor ecological conditions such as low oxygen, low pH and high organic matter content (Ojaveer et al., 2003; Rask, 1983) and is often a keystone species which is able to significantly influence freshwater communities (Closs et al., 2001). It is a generalist predator with a flexible, mostly carnivorous, diet consisting mainly of zooplankton, macroinvertebrates and fish for the larger individuals (Ojaveer et al., 2003; Rask et al., 2014). Perch is thus more sensitive to biotic than to abiotic conditions. The positive relationship between perch and pike biomass might be caused by the presence of a non-limiting mutual food item or ecological factor equally affecting both.

The positive relationship between bream and benthic macroinvertebrates can be explained by trophic interactions, as bream is a predominantly benthivorous species. Concerning the negative correlation between white bream biomass and rotifers, a study in Lake Ladik (Turkey) indicated that rotifers, although being the dominant zooplankton group in that lake, were the least prey choice by white bream among the zooplankton groups (Yağci et al., 2015; Yazicioğlu et al., 2017). The dominance of small zooplankters like rotifers might thus hint to detrimental conditions for white bream. In Vörtsjärvi *Chironomus plumosus* larvae, a strongly preferred food by bream and ruffe, form >80% of the macrozoobenthos biomass (Kangur et al., 2004; Kangur et al., 1999). The negative relationship between bream and summer water temperature could be due to O₂ depletion, water level decrease and cyanobacteria dominance that are concomitant with hot summers and might lead to fish kills (Kangur et al., 2005).

The main piscivorous fish species in Vörtsjärvi are pikeperch and pike which share similar prey preferences – ruffe and perch, (Kangur et al.,

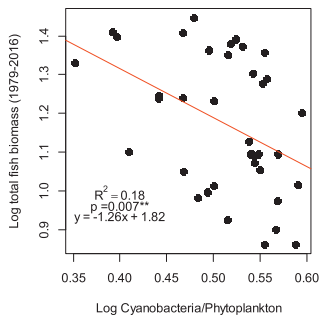


Fig. 3. Regression plot and equation of total fish biomass and share of cyanobacteria biomass in phytoplankton (n = 38).

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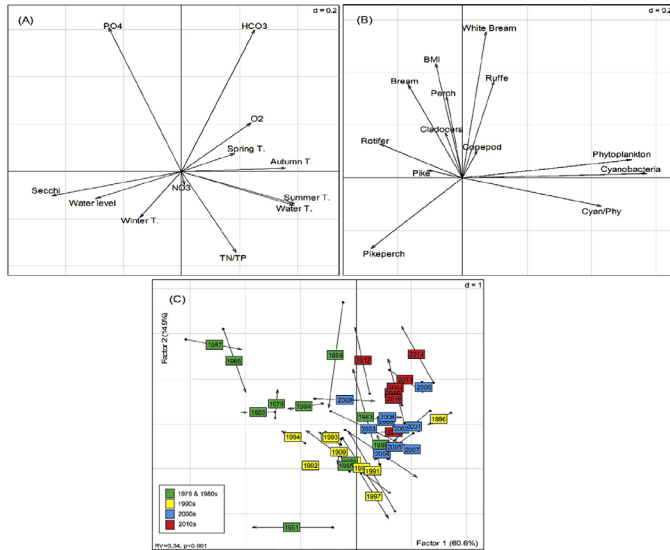


Fig. 4. Co-inertia analysis of the environmental variables (A) and organisms biomasses (B), the length and direction of vectors denote the weights of the variables in the first two factors. The panel C represents the concordance between environmental parameters and biomasses. The beginning and end of arrows denote the relative location of samples according to environmental parameters and biomass values, respectively; the numerical measure of concordance is given by RV-coefficient, for which p -value is evaluated by permutation test; percentage values indicate the proportion of the overall covariance between environmental parameters and biomass tables described by the first two factors. In the bottom panel, numbers denote different years ranging from 1979 to 2016.

2004). Besides these two species, bream, as a very abundant species in Vörtsjärvi, can also be among the food items of large-sized piscivores (Nilsson and Brönmark, 2000; Yazicioglu et al., 2018). Our RF results are in agreement with that as perch and bream biomasses were correlated with pike and pikeperch, respectively. The relationship is probably less relevant for smaller pikeperch individuals which dislike feeding on deep-bodied bream, because of gape limit (Didenko and Gurbyk, 2016; Dörner et al., 2007). Additionally, one study in Vörtsjärvi noted that bream was the last prey preference for pikeperch after ruffe, roach, perch, smelt and young pikeperch (P. Kangur et al., 2007). Associations between bream and pikeperch might in that case be caused by the similarity of ecological requirements (warm and eutrophic water) for these two species (K. Kangur et al., 2007; Sandström and Karås, 2002).

As nutrient limitation in lakes can be assessed by the TN/TP ratio (Bergström, 2010), a possible explanation for the positive relationship between pikeperch and TN/TP can be that high TP concentrations (and thus low TN/TP) promote cyanobacteria growth that are harmful to piscivorous fish through collapse of zooplankton and prey fish items (Cremona et al., 2018a). Macroinvertebrates are an important food item for pike fry but not for adults who switch to mainly piscivorous diet (Ojaveer et al., 2003). Therefore, the positive relationship between pike biomass and BMI might be explained by high densities of invertebrates creating favourable conditions for pike prey fish and thus pike themselves. However, the negative relationship between pike and summer temperature is more straightforward. Casselman (1996) noted that optimal temperatures for young and adult pike are, correspondingly, 19 °C and 22–23 °C with negative growth outcomes outside this range. High summer temperatures can lead to a O₂ depletion (hypoxia) which is one of main causes of summer fish kills in

freshwater fish species (Kangur et al., 2005; Kangur et al., 2013). Other researchers observed that due to high-temperature tolerance and ability to migrate to the deep water areas, pike could avoid direct climate change impact, although an indirect effect could occur through prey populations (Winfield et al., 2008). Conversely, some researchers have shown that water warming affected positively pike population growth rates although it was highly dependent on body size and vital rates (Vindenes et al., 2014).

Although no direct toxic or bloom-induced effect of cyanobacterial was observed in Vörtsjärvi, two mechanisms might explain the negative relationship between the proportion of cyanobacteria and total fish biomass. Firstly, the low feed quality of colonial cyanobacteria could trigger a bottom-up trophic cascade leading to a decline in fish recruitment (Zhang et al., 2013; Cremona et al., 2018a). Secondly, the decomposition of poorly edible cyanobacteria could deteriorate oxygen conditions in the shallow lake water column (Havens, 2008; Kangur et al., 2005).

Conclusion

Disentangling the relative influence of ecological factors on fish communities is not straightforward. Our study has shown that only a handful of ecological factors were important to predict fish population biomasses. Including fish life stages and commercial fisheries data into the model would probably improve the performance of future statistical models as it has improved mechanistic models (Cremona et al., 2018a). At the whole fish community level, the cyan/phy was the only significant (negative) predictor of biomass. Temperature increase that is detrimental to highly valuable commercial fish species such as pike but favours less valuable bream could cause shifts in the fish community

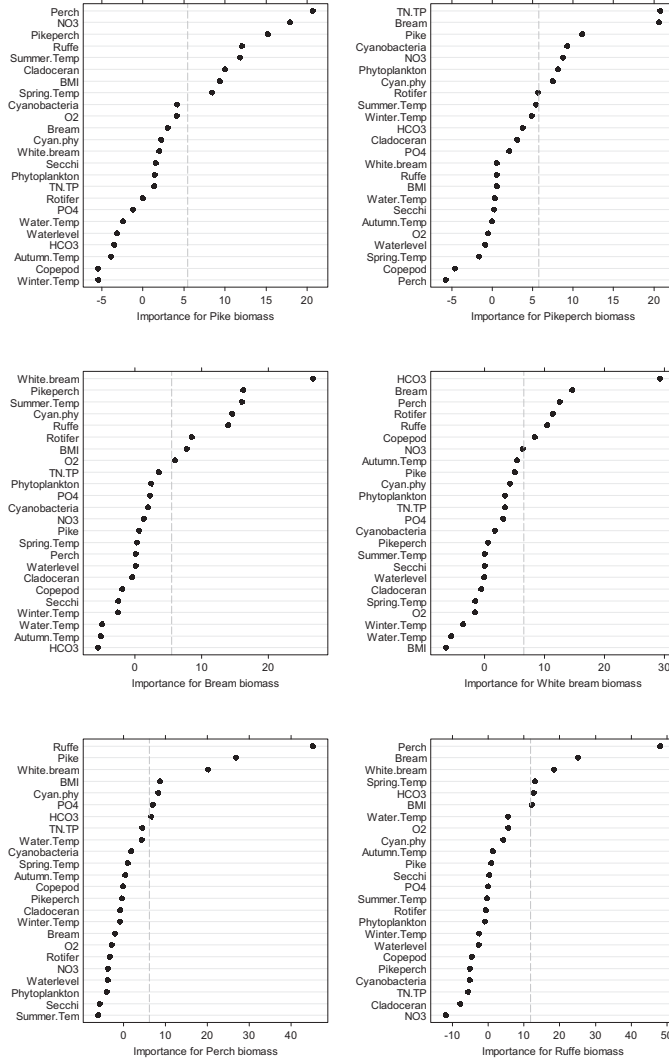


Fig. 5. Variables importance plots by Random Forests model for six fish species. Large positive numbers of importance and right side of the vertical dashed line indicate a high predictive capacity of a variable, whereas very small values and location left side of the line irrelevant for the response variables.

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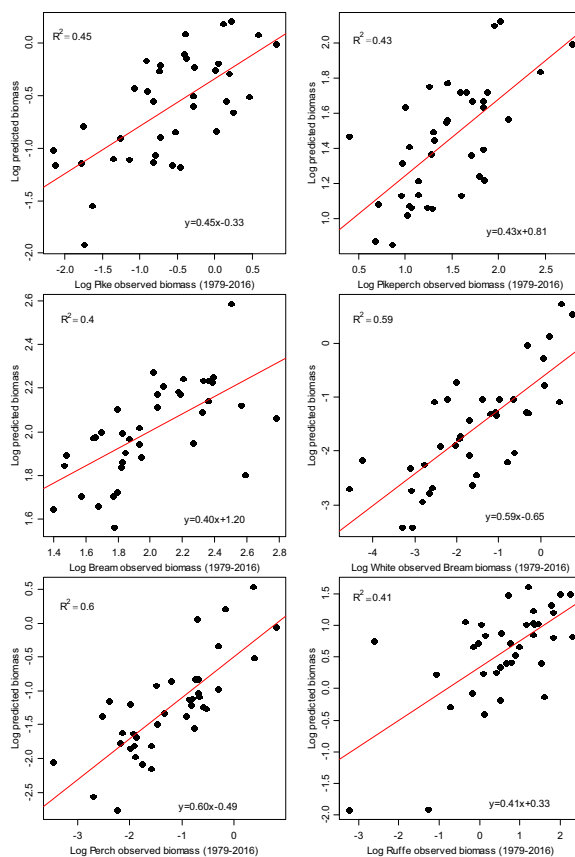


Fig. 6. Scatterplots of the predicted versus observed fish biomasses. Model descriptive variables are explained in Table 1 for each graph. Regression equation and R^2 are provided for each model ($n = 38$).

and undermine ecosystem services provided by the lake, such as commercial fishing. We recommend that any future stock assessment and management plan of Võrtsjärv should check the most influential abiotic factors such as TN/TP, HCO_3^- , summer and spring temperature that were shown to alter the structure of the food web and thus fish community composition. We also recommend that managers take into account interspecific relationships during fishing campaigns as perch and bream were very important for pike and pikeperch populations, respectively. Additionally, the abundance of benthic macroinvertebrates, for example, had a positive influence on species as trophically dissimilar as ruffe and pike. We hope that our findings will be useful and relevant for developing suitable conservation strategies to sustain the integrity of fish communities in the area.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jglr.2019.08.004>.

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How do environmental factors affect the yield of European eel (*Anguilla anguilla*) in a restocked population?

Priit Bernotas^{a,b,*}, Burak Öglü^a, Peeter Nöges^a

^a Chair of Hydrobiology and Fishery, Institute of Agricultural and Environmental Sciences, Estonian University of Life Sciences, Kreutzwaldi 5, 51006 Tartu, Estonia

^b Estonian Marine Institute, University of Tartu, Vanemuise 46a, 51010, Tartu, Estonia

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ABSTRACT

Restocking of European eel (*Anguilla anguilla*) is a widespread practice throughout Europe. Conditions during restocking activities and mortality related to restocking practices have been discussed, however, factors affecting these restocked populations afterwards are mostly not considered. In this study we used a machine learning method followed by generalized linear model to analyze long time eel restocking, commercial fishery and environmental data from Lake Võrtsjärv, Estonia, to detect whether significant relationships exist within these data. It was found that environmental parameters can have an effect on the commercial eel yield both retrospectively and during the particular fishing year. Considering that 7-year old eel was the most common age group in commercial catch, we introduced a 7-year gap between eel restocking and yield to study the most important abiotic and biotic factors during the first year of eel restocking that have an effect on the yield. According to our results, cyanobacterial biomass and summer water temperature during the year of restocking had the strongest negative impact on the yield 7 years after, while the number of restocked individuals and copepod biomass had a positive effect. During particular fishing year, however, the yield was most notably positively affected by total phosphorous concentration, number of individuals restocked 7 years before and metazooplankton biomass in the lake.

1. Introduction

Increasing anthropogenic pressures have multiple effects on freshwater ecosystems (Carpenter et al., 2011). Overexploitation of certain fish species, influence of different pollutants, habitat degradation, invasive species and physical modification of flow characteristics, each play a role in changing conditions both in freshwater lakes and rivers (Dudgeon et al., 2006). Most of these factors have a direct or indirect impact on the rise of such phenomena as eutrophication, dominance of cyanobacteria, increase in phosphorous concentrations, and high nitrogen fixation rates (Hecky et al., 2010; Mugidde et al., 2003). Besides, freshwater systems are also heavily affected by climate change (Mooij et al., 2005; Woodward et al., 2010). Global warming has been found to have a strong impact on eutrophication of fresh water lakes (Anneville et al., 2015) and has a positive influence on growth rates, dominance, distribution and activity of harmful cyanobacteria (Paerl and Huisman, 2009, 2008). The negative effect of hypoxia caused by eutrophication and cyanobacterial blooms on benthic fish species has been widely discussed in scientific literature (Diaz and Rosenberg, 1995; Paerl and Huisman, 2009; Pörtner and Peck, 2010).

A benthic species such as the European eel (*Anguilla anguilla*) is known to inhabit a wide variety of habitats from marine to fresh waters (Tesch et al. 2003). While eel is being a common species throughout Europe, its stocks have been declining rapidly during the last 40–50 years (Dekker, 2016). It is known that anthropogenic factors such as habitat loss, water pollution, commercial and recreational fisheries and migration obstacles (dams, weirs, pumping stations) play an important role in the decline (Dekker and Beaulaton, 2016). These factors affect eels most in the continental phase of the life cycle while environmental factors, such as climate change, mostly during the oceanic phase (Drouineau et al., 2018). However, as eels can spend most of their life in fresh water (Tesch et al., 2003) the environmental stressors affecting this period need to be studied thoroughly.

Eels may reach fresh waters via migration through river systems or by restocking. In Estonia, most of the fresh water eel population relies on annual restocking programme (Bernotas et al., 2016). While eels are known to be able to survive in unfavourable conditions (Tesch et al. 2003), their distribution in a water body still depends on habitat quality and accessibility as well as population characteristics (Laffaille, 2003). However, studies on environmental parameters affecting glass eels or

* Corresponding author.

E-mail addresses: pbernotas@emu.ee (P. Bernotas), ogluburak@gmail.com (B. Öglü), Peeter.Noges@emu.ee (P. Nöges).

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elvers following restocking are hard to find.

For implementation of conservation measures, describing of changes in fish biomass and population dynamics or experimenting with “what if” scenarios, the fisheries science has been using different modelling approaches (Christensen and Walters, 2004; Method and Wetzel, 2013; Pauly et al., 2000; Thorson, 2019). As complex freshwater ecosystems, such as large lakes, have numerous parameters influencing their fish communities, ecosystem modelling is the most suitable approach for predicting the potential effects of these interactions (Ficke et al., 2007). In Estonian freshwater fisheries context, modelling has been used to determine which abiotic and biotic factors control the changes in fish biomass in Lake Võrtsjärv (Õglü et al., 2019).

The aim of this study was to investigate what are the most important environmental factors affecting the restocked eels directly after restocking and later in their growing phase. It was also assumed that the number of specimens restocked has the strongest influence on the yellow eel stock capacity. We asked what affects most the commercial yield, which indicates the stock size of eels 7 years after restocking when the age class becomes most prominent in the catches – the number of specimens restocked, the conditions at restocking or the conditions of the particular fishing year.

2. Material and methods

2.1. Study area

Võrtsjärv is a large, but shallow, eutrophic and turbid water lake. The surface area of the lake is 27 000 ha, making it the second largest lake in the Baltic States (Järvet, 2004). Its drainage basin (3374 km²) is situated in the Central Estonian depression of preglacial origin and is connected to the drainage basin of Lake Peipsi (47,800 km²) through the outflowing Emajõgi River (Järvet, 2004). The small mean and maximum depths, 2.8 m and 6.0 m, respectively, make Võrtsjärv responsive for environmental changes. The water is alkaline and due to turbidity the visibility is low. The lake is covered with ice on average for 135 days, lasting from November until April (Tõnno et al., 2016). No significant trends in the ice cover duration were found (Nöges and Nöges, 2014). According to the Water Framework Directive typology, Võrtsjärv is a large calcareous shallow lake with most ecological status parameters falling into either “good” or “moderate” class (Tuvikene et al., 2011). During ice-free period, Secchi depth does not exceed 1 m. Phytoplankton is dominated by eutrophic and highly shade tolerant cyanobacteria from the genus *Limnothrix* (Jananian et al., 2019). According to the long-term annual phytoplankton primary production (208 ± 27 gC m⁻² year⁻¹), Võrtsjärv is close to the nutrient-saturated production boundary for lakes determined by latitude where light limitation has the leading role (Nöges et al., 2011).

2.2. Fisheries

One lamprey species (*Lampetra planeri*) and 31 fish species permanently inhabit Võrtsjärv (Järvalt, 2003; Pihu, 1998). Eel, pikeperch (*Sander lucioperca*), pike (*Esox lucius*), and bream (*Abramis brama*) are the most important commercial species in the lake, while perch (*Perca fluviatilis*) and burbot (*Lota lota*) are of secondary commercial interest (Järvalt, 2003; Nöges et al., 2018).

The eel production of Võrtsjärv is entirely based on restocking of glass eels or elvers. The restocking programme started in 1956 and has continued to present day. Since 1980, restocking of eel has been annual (excluding years 1986, 1989, 1990 and 1993; Bernotas et al., 2020). The number of restocked individuals has been dependent on available financial resources and thus directly connected to the glass eel market prices (Bernotas and Silm, 2019). Eel is targeted by commercial fishery using fyke nets (mesh size in the cod end = 18 mm) with the legal landing size being TL ≥ 55 cm. Commercial harvest is due to the legal

size dominated by female yellow eels. The number of fyke nets used by the fishermen has stayed on a stable level (from 300 to 360) since 1971 (Nöges et al., 2018). The eel fishing season lasts from April to October. No data on the number of fishermen or companies is available for the Soviet time. The number of fishermen or companies operating the gear has changed during the last 10 years due to companies selling some of the licences however the number of gear has stayed the same (N = 322).

For calculation purposes, the amounts of restocked elvers were converted into glass eel equivalents (GEE) according to formula by Dekker (2015):

$$\text{glass eel equivalents}_{\text{year-age}} = \text{elvers}_{\text{year, age}} \times \exp^{+M \times \text{age}}$$

where year = the year of observation, age = the mean age, and M = natural mortality between the glass eel and the elver stage. For M , an average value of 0.10 per year was used (Dekker, 2015).

2.3. Data collection

The data used in the models derives from 3 different sources. The commercial fisheries data (tonnes) is collected annually by the Ministry of Rural Affairs, the eel restocking data (numbers, kilograms) annually by the Ministry of Environment and the data on environmental variables by Estonian University of Life Sciences. The commercial fisheries and eel restocking data used in this study dates back to 1964 and 1956, respectively (Table 2). The data on water chemistry, phyto- and zooplankton biomass is available since 1964 and is collected at least once per month (Nöges et al., 2018). Benthic macroinvertebrate (BMI) samples are taken during ice-free period and sampled alive, processed using 70 % alcohol and then dried and weighted (Kangur et al., 1998). The collected data on BMI were converted into total biomass.

2.4. Data analyses

The glass eels or elvers restocked in the lake are called “young of the year” (YOY) and the eels caught in the commercial fishery – “yellow eel”. According to the data collected in the last 5 years, the 7 year age group makes up 20 % of the harvest, followed by 8 (17 %) 9 (16 %) and 6 (15 %). 2019 data proved that approximately 56 % of the harvest is FII stage yellow eels, 35 % FIII non migrating silver eels and 8% migrating silver eels (Bernotas and Silm, 2019). To determine the time of the most prominent appearance of the restocked eel in catches, correlations between YOY and yellow eels were also calculated shifting the series by 0–12 years relative to each other. The strongest correlation corresponded to a gap of 7 years (Fig. 1). Therefore, the environmental and feeding conditions 7 years before the catch were considered as those that affected the YOY stage. For yellow eels, the environmental parameters from the year of harvest were used, while restocking data was used with a 7-years gap. Statistical analyses were performed using R project 3.5.3 (R Core Team, 2019).

2.5. Variable selection

To detect collinearity among the variables and interactions, Variance Inflation Factor (VIF) was used for testing the presence of the inflated variance of regression coefficients due to lack of independence between the variables in the model (O'Brien, 2007). We used threshold of 8 that, according to literature suggestion, has been considered sufficient to avoid the collinearity (Babak, 2015; Cremona et al., 2018; Feld et al., 2016; Smith et al., 2007) and variables which exceeded this threshold value were excluded from further analyses. In addition, to assess statistical relationship between environmental parameters and eels, Pearson correlation analysis was applied and ‘corplot’ used to illustrate the correlation coefficients (Wei and Simko, 2013). Non-parametric regression tool and machine learning method,

Table 2
Restocking/landings year, number of glass eel equivalents (GEE) restocked, number of specimens restocked per hectare of the lake and annual landings of Vortisj ar commercial fishery.

Year	Restocking (N GEE/sp)	N sp/ha	Landings (kg)
1956	200,000	7.4	ND
1957	0	0.0	ND
1958	0	0.0	ND
1959	0	0.0	ND
1960	60,000	2.2	ND
1961	0	0.0	ND
1962	900,000	33.3	ND
1963	0	0.0	ND
1964	200,000	7.4	3000
1965	700,000	25.9	300
1966	0	0.0	1900
1967	0	0.0	2700
1968	1,400,000	51.9	2900
1969	0	0.0	5000
1970	1,000,000	37.0	6500
1971	0	0.0	6500
1972	100,000	3.7	16,400
1973	0	0.0	21,300
1974	1,800,000	66.7	18,700
1975	0	0.0	36,900
1976	2,600,000	96.3	41,600
1977	2,100,000	77.8	50,000
1978	2,700,000	100.0	45,000
1979	0	0.0	19,000
1980	1,300,000	48.1	17,800
1981	2,700,000	100.0	16,400
1982	3,000,000	111.1	10,800
1983	2,500,000	92.6	24,600
1984	1,800,000	66.7	66,700
1985	2,400,000	88.9	71,900
1986	0	0.0	55,600
1987	2,500,000	92.6	61,200
1988	198,931	7.4	103,700
1989	0	0.0	47,600
1990	0	0.0	56,100
1991	2,000,000	74.1	48,500
1992	2,500,000	92.6	31,000
1993	0	0.0	49,200
1994	1,900,000	70.4	36,900
1995	165,776	6.1	38,800
1996	1,400,000	51.9	34,100
1997	900,000	33.3	40,300
1998	500,000	18.5	21,800
1999	2,300,000	85.2	37,400
2000	1,100,000	40.7	38,800
2001	486,275	18.0	37,600
2002	314,974	11.7	20,400
2003	450,910	16.7	26,400
2004	533,798	19.8	20,100
2005	364,706	13.5	17,600
2006	364,706	13.5	19,900
2007	320,500	11.9	21,500
2008	193,405	7.2	20,500
2009	464,172	17.2	13,600
2010	198,931	7.4	10,300
2011	713,672	26.4	11,300
2012	902,621	33.4	12,600
2013	883,674	32.7	12,700
2014	2,716,850	100.6	13,300
2015	1,600,500	59.3	12,300
2016	1,093,298	40.5	13,000
2017	307,238	11.4	13,800

Random Forests (RF) was performed to select most important parameters for the young of the year and yellow eels with 1000trees by using 'package RandomForestSRC' and to estimate the variables importance 'gg_vimp' function was used. (Feld et al., 2016; Ishwaran and Kogalur, 2017).

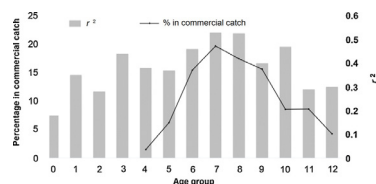


Fig. 1. Bar plot of correlation coefficients of back calculations between yield and number of individual eels restocked (corresponds to the scale on right) and most numerous age groups in the commercial catch (Bernotas and Silm, 2019; corresponds to the scale on left).

2.6. Model construction and selection

Generalized linear models (GLM) were performed for YOY and yellow eels with the four predictors which were selected as most important parameters according to RF. Model parameters were centered before GLM, to be eligible for comparison. Interaction and additive effects were tested. Moran's I test was applied on the residuals to test temporal autocorrelation by using the 'ape' package in R (Paradis et al., 2019). The results of Moran I < 0.1 values indicate the absence of significant temporal correlation (Paradis, 2019). Akaike's Information Criterion small-sample equivalent (AICc) was used for evaluation and selection of the model (Akaike, 1973; Brewer et al., 2016). To compare and ordered the models according to AICc values 'dredge' function was applied by using 'MumIn' Package in R (Barton and Barton, 2015). Models were selected among the range of delta AICc ($\Delta AICc$) > 2 that are equally supported (Burnham and Anderson, 2004). R² values were considered as goodness of fit of models and model explanatory.

3. Results

3.1. Importance and relationship of selected variables

Significant Pearson correlations for YOY eel (Fig. 2A) were found with total phytoplankton biomass ($r = -0.59, p < 0.05$), biomass of cyanobacteria ($r = -0.69, p < 0.001$) and summer water temperature ($r = 0.43, p < 0.05$), while the commercial yield of yellow eels (Fig. 2B) had significant correlations with biomasses of metazooplankton ($r = 0.39, p < 0.05$), phytoplankton ($r = -0.36, p < 0.05$), cyanobacteria ($r = -0.34, p < 0.05$), autumn water temperature ($r = -0.33, p < 0.05$) and total phosphorous concentration ($r = 0.38, p < 0.05$).

The Random Forest test indicated that the most important parameters during the YOY stage affecting yellow eel density were cyanobacteria biomass, summer water temperature and copepod biomass whereas the number of restocked YOY ranked second after cyanobacteria (Fig. 3). The annual eel harvest rate was most importantly affected by TP (total phosphorus) and metazooplankton in the catching year, and again the restocking numbers 7 years earlier was the second important parameter after TP (Fig. 3).

Food sources during the YOY stage (rotifer, cladoceran, metazooplankton) except for copepods were among the least important parameters determining further eel catch. For yellow eels, water physical parameters were least important (secchi, water level, average water temperature). Although, metazooplankton was among the least important parameter for YOY, it was one of the most important parameter for the yellow eels.

3.2. Model performance

The GLM model construed for both YOY and yellow group of eel

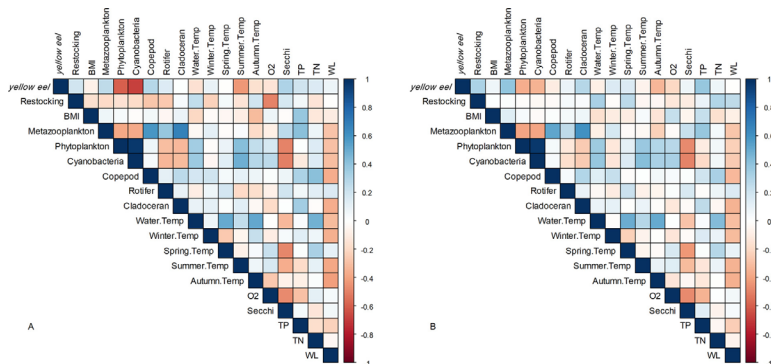


Fig. 2. Pearson correlation of the commercial eel yield with restocking numbers and environmental variables during the YOY stage (7 years before the catch; A) and in the year of catch (yellow stage; B). Blue gradients indicate positive correlations and red gradients indicate negative correlations while the intensity of the gradient expresses the correlation strength.

with additive and interaction effects for selected parameters ordered by AIC values is given in Supplementary Table 1. In this study, significant autocorrelation was not detected in any models.

Temporal autocorrelation was detected for neither life stage, and AICc values varied from 68.5–117.7 for YOY eel and from 93.1–124.7 for yellow eel. Only $\Delta AICc < 2$ were considered as equally important. Five models were in the range of delta AICc 2 and R^2 varied 0.569 to 0.781 for YOY, while five models were found in the range of delta AICc 2 and R^2 varied from 0.540 to 0.640 for yellow eels. Model number 8 and model number 592 were selected because of low df values, strong r^2 and as it took also restocking as a parameter into account. The model outcome revealed that 59 % and 56 % of the variability in YOY and yellow eels, respectively, could be explained by the selected parameters that were used in GLM models (Table 1, Fig. 4).

Table 1
Best Generalized Linear Models for eel catches based on restocked number and conditions during YOY and yellow stages.

Stage	Model equation and parameters	df	R^2	AICc
YOY	Eel ~ Copepod*(0.357) + Cyanobacteria*(-0.668) + Stocking*(0.170) + $(5.8 \cdot 10^{-15})$	5	0.59	69.55
Yellow	Eel ~ Metazooplankton*(0.239) + Stocking*(0.168) + TN*(0.240) + TP*(0.167) + Metazooplankton:TP*(0.295) + TN :TP*(-0.423) - 0.118	8	0.56	94.5

4. Discussion

Our results showed that 59 % of the variability in the YOY survival could be explained by the restocked number and the conditions during

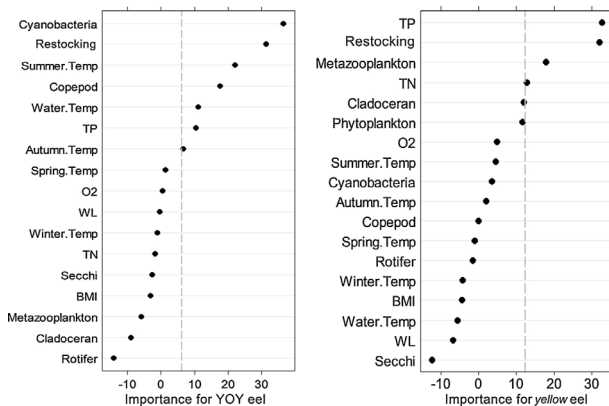


Fig. 3. Dot plots of Random Forest model ranking variables for commercial eel catch by importance: A - during YOY stage (7 years before catch) and B - during yellow stage (in the year of catch). Right side of the threshold (vertical dashed line) considered highly important variables for each group, whereas negative and small values are irrelevant for the YOY and yellow eels.

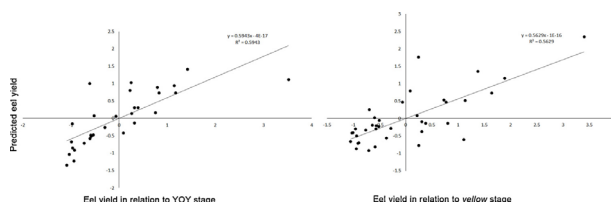


Fig. 4. Centered scatterplots of the predicted eel yield (t) versus eel yield during YOY stage (7 years before catch; t) and eel yield during yellow stage (in the year of catch; t). Regression equation and R^2 are provided for each model.

the year of restocking, whereas 56 % of the variability in the harvest rate of the restocked eels by the restocked number and the conditions 7 years later during harvest.

We demonstrated that the number of eels restocked in a given year has a very strong effect on the yield 7 years later highlighting the critical importance of growth conditions during the first lake year for the glass eels. While being introduced to a water body, eels sustain extra stress making them more vulnerable to environmental stressors. It has been suggested that early life-history stages of fish are most affected by environmental changes (Rijnsdorp et al., 2009). Presumably glass eels are subject to vast mortality during the first few months after recruitment (Lambert, 2008). Also, handling during restocking activities (Josset et al., 2015) and predator attacks directly after restocking (Ovidio et al., 2015) could affect the glass eel mortality. In the context of Vörtsjärv, gulls (*Laridae*) have been observed to prey on glass eel while restocking has taken place during daylight (*Unpublished observation, P.B.*). Glass eels were also discovered in the stomachs of perch right after restocking activities on Vörtsjärv (*Unpublished data, P.B.*). Unfortunately, we could not add predation as a factor into the model due to lack of data available.

Our results showed that the prevalence of cyanobacteria in the water body has the strongest negative effect on YOY. Restocking of eels in Vörtsjärv takes usually place in spring when cyanobacterial populations are starting to grow and their abundance is still low. However, rapid growth of cyanobacteria in early summer results in peak of cyanobacterial biomass in mid-summer (Nöges et al., 2004). Observations have shown that when glass eels are introduced to a water body, they prefer shallow sheltered habitats where water movement is low (Ovidio et al., 2015). In a context of a large lake, this counts for littoral areas where cyanobacterial scum formations or benthic populations are known to form (Malbrouck and Kestemont, 2006). The period of time necessary for restocked eels to recover from stress associated with transport and introduction to a water body is not known neither is the time it takes for restocked eels to start feeding. So during the first lake year, glass eels grow side by side with the increase of cyanobacterial populations which means the latter can have an effect on the growth of restocked glass eels. A study by (Engström-Öst and Isaksson, 2006) showed that the feeding of pike larvae decreased in the presence of cyanobacteria. It could very well be that filamentous cyanobacterial formations have similar effect on the behavior of glass eels. Glass eels may feed on various food sources in fresh water habitats. A study carried out by (Belpaire et al., 1992) indicated that in freshwater ponds the most important prey for glass eels were Cladocera and Ceratopogonidae. Both these taxa are also very common in the littoral zone of Vörtsjärv (Kangur et al., 2004; Nöges et al., 2004), making them theoretically a preferred food source for restocked glass eels. It is known that abundance of cladocerans can be affected negatively by the formation of cyanobacterial blooms or by the rise of cyanobacterial biomass in the lake (Ghadouani et al., 2003; Gliwicz, 1990). Also, through increasing the complexity of a habitat, filamentous algae have a negative influence on the foraging success of juvenile fish (Pihl et al.,

1995). Similar negative influence from cyanobacteria has been observed with BMI (Krivoshchina, 2008). Our results showed that neither cladoceran abundance nor BMI impacted restocked glass eels significantly. However lower feeding success of fish larvae (such as glass eels) can depend on lower visibility (Utne-Palm, 2002) or clogging of the gills during cyanobacterial blooms (Engström-Öst and Isaksson, 2006). So years with unfavourable environmental conditions (such as cyanobacterial prevalence) during restocking year have a stronger effect on the yield than just smaller number of restocked individuals.

The “copepod” effect could be interpreted through copepods being an intermediate host for swim bladder parasite *Anguillicola Crassus* (Hubbard et al., 2016; Kirk, 2003). It has been found that crustaceans serve as intermediate parasite hosts for smaller (< 20 cm) eels; (Thomas and Ollevier, 1992) and glass eels might be infected as soon as they start feeding (Nimeth et al., 2000). Surprisingly it has been found that infected eels can have greater body length and mass compared to uninfected specimens (Lefebvre et al., 2013). The aforementioned study also hypothesizes that as actively foraging individuals are more likely to get infected they are also more likely to get caught by passive fishing gear (Lefebvre et al., 2013). In Vörtsjärv 49 % of the legal sized eels are known to be infected with *A. Crassus* (Bernotas and Silm, 2019). So during years with high copepod biomass, restocked glass eels may have an increased consumption of copepods which over our studied 7 year cycle has a positive effect on the yield but also reflects in the high ratio of infected eels in the population.

Effectiveness of fishery can be described by catchability which is a combined result of fish abundance and fishing effort (Arreguin-Sánchez, 1996). Thus, it could be assumed that at a constant fishing effort, catchability be defined by fish abundance. However, environmental parameters and fish behavior also influence the catchability (Hilborn and Walters, 2013; Hubert and Pope, 2012; Rogers et al., 2003). Our results indicated that some environmental factors during the fishing year have significant influence on the commercial yield of eel. Most notably, TP concentration in the fishing year had the strongest effect on yellow eel harvest. High TP concentrations in water give evidence of eutrophication and thus can be related to low fish diversity (Naigaga et al., 2011), higher abundance of cyprinids such as Common carp (*Cyprinus carpio*) (Carol et al., 2006) a decline in piscivores (Du et al., 2015) or a decrease in *Anguilla* spp. catch and abundance (Rönnerberg and Bonsdorff, 2004; Thomas et al., 1993). However, in case of eel, our results were opposite. Instead of decreasing yield during the years with high TP concentrations, it increased. This could be explained with the nature of the local fishery. Only fyke nets are used for catching eel on Vörtsjärv. When fishing with passive gear, first the fish must encounter the gear (Hubert and Pope, 2012). This means that the commercial yield in Vörtsjärv is directly connected to fish movement that may be stimulated by high TP concentrations. One plausible explanation could be that during years with high TP concentrations in the water, benthic habitats become uninhabitable during high growth periods because of hypoxia (Correll, 1998) making eels leave their habitat in search for more suitable conditions. Still the exact reason behind the rise in eel

catch during high TP concentrations in Vörtsjärv needs to be studied further.

The immediate positive effect of metazooplankton abundance on the yellow eel stock may reflect a decline in planktivorous fish and their relationship to diet changes of benthivorous fish. Bream, roach (*Rutilus rutilus*) and perch are all abundant species in Vörtsjärv (Järvalt, 2003). It was found that with a decrease in planktivorous fish biomass, changes in the diet of bream (TL < 300 mm), roach (larger size classes) and perch (TL = 120–150 mm) were observed (Persson and Hansson, 1999). All of the aforementioned groups had a tendency to switch from pelagic to benthic prey when planktivorous fish communities were altered (Persson and Hansson, 1999). In Vörtsjärv macroinvertebrates are a preferred food source for eels (Kangur et al., 1999; Teesalu, 2019), and they adapt their diet to the most available food source (Bouchereau et al., 2009). Increased food competition from other species may increase the migrations of eels within a water body however whether such migrations increase the possibility of being caught by passive fishing gear needs to be addressed in future studies.

Interactions of environmental factors such as TP with metazooplankton and TN with TP during the harvest year may also affect the yellow eel harvest rate. While the positive impact of the TP and metazooplankton interaction can be explained by the effects discussed in the preceding two paragraphs, the negative influence of TN:TP interaction can also be connected to the TP concentration. Higher TN:TP values relate to oligotrophic lakes which obtain the N and P from undisturbed sources that export less P than N while lower TN:TP values are connected with meso- or eutrophic water bodies (Downing and McCauley, 1992). High TN:TP ratio means smaller TP concentration in the water body which in turn has a negative effect on the yellow eel harvest rate.

4.1. Study limitations

Although data on restocking densities is hard to find we assumed for this study the restocking densities in Vörtsjärv to be low. The average number of GEE restocked per hectare during the study period was 33 specimens (Table 2). Assuming a mean weight of a specimen being 0.3 g this means a restocking density of 0.00099 g per m². As natural mortality of restocked glass eels or elvers is very difficult to observe in the wild we assumed a constant annual rate of $M = 0.1$. Due to lack of data from most of the study period assumption on a constant growth rate was also made.

5. Conclusion

Based on the results of our study it can be concluded that environmental conditions in a water body during the time of restocking play an important role in determining the future yields of eel. It was concluded that during the year of the harvest, environmental factors affected the yield to a lesser extent. Although we concentrated on predicting the impact on commercial yield, in conditions of a steady fishing effort like in Vörtsjärv where the number of fishing gear has remained constant, the yield could very well represent also eel biomass. The parameters most affecting restocked eels vary likely between different water bodies but in case of eutrophic lakes, the leading factors described in the present study should be studied further to optimize future eel restockings. Also if there is a choice between different water bodies where to restock eels and if data is available it would be recommended to take the relationships discussed in this study into consideration to account for either a positive or negative effect on the restocked eel population.

CRedit authorship contribution statement

Priit Bernotas: Conceptualization, Methodology, Investigation, Writing - original draft, Writing - review & editing, Supervision, Project

administration, Funding acquisition. **Burak Ögütü:** Conceptualization, Methodology, Software, Writing - original draft, Visualization. **Peeter Nõges:** Writing - original draft, Writing - review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.fishes.2020.105649>.

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CURRICULUM VITAE

Name: Burak Öglü
Date of birth: 29.06.1990
E-mail: Ogluburak@gmail.com
Address: Chair of Hydrobiology and Fishery,
Institute of Agricultural and Environmental Sciences,
Estonian University of Life Sciences, Kreutzwaldi 5,
51006 Tartu

Education:

2015 – 2021 PhD studies in Estonian University of Life Sciences
2012 – 2014 MSc in department of biology, Institute of Science,
Muğla Sıtkı Koçman University, Turkey
2008 – 2012 BSc in department of biology, Science Faculty, Muğla
Sıtkı Koçman University, Turkey

Professional employment:

2019 – ... Estonian University of Life Sciences, Researcher
2017-2018 Estonian University of Life Sciences, Junior Researcher

Research interests:

FIELD OF RESEARCH: 1. Biosciences and Environment; 1.4.
Ecology, Biosystematics and –physiology
CERCS SPECIALTY: B260 Hydrobiology, marine biology, aquatic
ecology, limnology

Professional training:

International Summer School on Lake Ecology and Management,
Gauja National Park (Latvia), 24 August – 2 September 2017.
gRaphics: Data-driven storytelling workshop, 1 February 2021, Finland,
Oikos Conference.

Membership:

2017–... Individual member of the Global Lake Ecological
Observatory Network (GLEON)
2017–2021 Member of International Limnological Society (SIL)
2017–2021 Member of Association for Science of Limnology and
Oceanography (ASLO)
2021–... Member of Nordic Society Oikos

Publications:

Öğlü, Burak; Bhele, Upendra; Järvalt, Ain; Tuvikene, Lea; Timm, Henn; Seller, Siim; Haberman, Jutta; Agasild, Helen; Nõges, Peeter; Silm, Maidu; Bernotas, Priit; Nõges, Tiina; Cremona, Fabien (2020). Is fish biomass controlled by abiotic or biotic factors? Results of long-term monitoring in a large eutrophic lake. *Journal of Great Lakes Research*, 46 (4), 881–890. DOI: 10.1016/j.jglr.2019.08.004.

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Presentations at international conferences:

Bhele, Upendra; Öğlü, Burak; Nöges, Peeter; Nöges, Tiina (2019). Modelling the food web structure of a large shallow lake. Symposium for European Freshwater Sciences: 11th Symposium for European Freshwater Sciences, Zagreb, Croatia, June 30–July 5, 65–65.

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ELULOOKIRJELDUS

Nimi: Burak Öglü
Sünniaeg: 29.06.1990
E-post: Ogluburak@gmail.com
Aadress: Hüdrobioloogia ja kalanduse õppetool, Põllumajandus- ja keskkonnainstituut, Eesti Maaülikool, Kreutzwaldi 5, 51006, Tartu

Haridustee:

2015 – 2021 doktoriõpe rakendusbioloogia erialal, Eesti Maaülikool
2012 – 2014 MSc in department of biology, Institute of Science, Muğla Sıtkı Koçman University, Türgi
2008 – 2012 BSc in department of biology, Science Faculty, Muğla Sıtkı Koçman University, Türgi

Töökogemus:

2019 – ... Eesti Maaülikool, teadur
2017-2018 Eesti Maaülikool, nooremteadur

Teadustöö põhisuunad:

VALDKOND: 1. Bio- ja keskkonnateadused; 1.4. Ökoloogia, biosüsteematika ja –füsioloogia
CERCS ERIALA: B260 Hüdrobioloogia, mere-bioloogia, veeökoloogia, limnoloogia

Erialane enesetäiendus:

International Summer School on Lake Ecology and Management, Gauja rahvuspark (Läti), 24. august – 2. september 2017.
gRaphics: Data-driven storytelling workshop, 1. veebruar 2021, Soome, Oikos Conference.

Teadusorganisatsiooniline tegevus:

2017–... Global Lake Ecological Observatory Network (GLEON) liige
2017–2021 International Limnological Society (SIL) liige
2017–2021 Association for Science of Limnology and Oceanography (ASLO) liige
2021–... Nordic Society Oikos liige

Publikatsioonid:

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Ettekanded rahvusvahelistel konverentsidel:

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VIIS VIIMAST KAITSMIST

KAIRI MAILEHT

FÜTOPLANKTON JÄRVEDE SEISUNDI INDIKAATORINA
PHYTOPLANKTON AS ECOLOGICAL QUALITY INDICATOR OF LAKES

Professor Emeritus **Ingmar Ott**, juhtivteadur **Peeter Nõges**

19. veebruar 2021

PAUL FRIDTJOF MÓTSKÜLA

ELEKTRO- JA PILTDIAGNOSTIKA TÄIENDAVALD RAKENDUSED KOERTE
SÜDAMEHAIGUSTE DIAGNOOSIMISEL NING PROGNOOSIMISEL
CONTRIBUTION TO THE DIAGNOSIS AND PROGNOSIS OF CANINE CARDIAC
DISEASE THROUGH ELECTRODIAGNOSTICS AND DIAGNOSTIC IMAGING

Professor **Toomas Orro**, Professor **Virginia Luis Fuentes** (The Royal Veterinary College, UK),
Professor **David Connolly** (The Royal Veterinary College, UK) ja doktor **Ranno Viitmaa**

8. märts 2021

JONATHAN MARTIN WILLOW

TIAKLOPRIIDI, TAIMSETE EETERLIKE ÕLIDE JA KAHE-AHELALISE RNA
RAKENDAMISE VÕIMALUSED HIILAMARDIKATE KESKKONNASÄSTLIKUS
TÕRJES

EXAMINING THIACTOPRID, ESSENTIAL OILS AND DOUBLE-STRANDED RNA
FOR POTENTIAL USE IN BIOSAFE MANAGEMENT OF POLLEN BEETLE

Professor **Eve Veromann**, professor **Guy Smagghe**

12. aprill 2021

MARIA SOONBERG

GRUPEERIMISE MÕJU PIIMALEHMADE KÄITUMISELE JA HEAOLULE
REGROUPING EFFECTS ON BEHAVIOUR AND WELFARE OF DAIRY COWS

Professor **David Arney**, doktor **Marko Kass** ja professor **Tanel Kaart**

26. aprill 2021

MARIANA MAANTE-KULJUS

VIINAPUU (VITIS SP) SAAGI KÜPSUSNÄITJAD
MATURITY PARAMETERS OF GRAPEVINE (VITIS SP) YIELD

Professor **Kadri Karp**, dotsent **Leila Mainla**, dotsent **Ele Vool**

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