

**SEVENTH FRAMEWORK PROGRAMME**

**THEME 6: Environment (including Climate Change)**



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Freshwater Ecosystems**

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along a European climate gradient**

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## 1. Abstract

Recent research related to biodiversity is very much driven by the realisation that biodiversity is declining at an alarming rate worldwide across all ecosystems through anthropogenic impacts such as land use, eutrophication, and global warming. We provide a number of case studies documenting the role of environmental forces such as water temperature, changes in the thermal regime of lakes, changes in water level, nutrients or salinity on aquatic species composition (plankton, macroinvertebrates, fish), biomass development (plankton, periphyton) and biodiversity (plankton, fish). The case studies cover a north/south European gradient.

We found climate induced changes in the thermal regime (extension of thermally stratified events during summer) of a polymictic lake to positively affect algal mass development in favour of cyanobacteria dominance, accompanied by a switch to nitrogen fixing cyanobacteria species. This led to a higher proportion of nitrogen fixation- and as such to a change in the ecosystem functionality. Changes in water level turned out to be the major driving forces for determining a shift in phytoplankton species composition in a shallow non stratified lake. High water levels accompanied by high water color and a deterioration of light conditions were estimated as the main driving force underlying the shift towards a highly shade tolerant phytoplankton community dominated by *Limnithrix redekei* and *L. planktonica*.

The diversity of fish communities were studied in 1632 lakes across 11 European countries. The study revealed that local fish species richness and diversity were related mainly to morphometric and (bio) geographical/climatic variables. Larger and deeper lakes in warm areas tended to be the most species rich and diverse. Fish density was related mainly to anthropogenically driven productivity but also was sensitive to geographical/climatic factors. Thus, warmer and shallower lower-altitude European lakes, which are usually more eutrophic, had higher fish densities than cold and deeper higher-altitude lakes. Fish size increased with altitude and declined with increasing seasonality and temperature. The potential effects of temperature, salinity and fish on the plant-associated macroinvertebrate community structure and biodiversity were studied in cold-temperate and Mediterranean shallow brackish lakes. Plant-associated macroinvertebrates and free-swimming macroinvertebrate predators were more abundant and the communities richer in species in the cold compared to the warm climate, most probably as a result of differences in fish predation pressure.

Water temperature turned out to be the most important driver to positively affect periphyton growth in lakes exhibiting high and low nutrient concentrations across a north/south European. The slope of the regression between water temperature and periphyton biomass suggested that, for every degree increase in water temperature, summer periphyton biomass was stimulated by 42%.

Overall, in most case studies a modulation of direct temperature, salinity, and water level effects by food web interactions was seen. Thus, care should be taken when predicting the combined effect of changes in multiple factors from their individual effects.

## 2. Introduction

Recent research related to biodiversity is very much driven by the realisation that biodiversity is declining at an alarming rate worldwide across all ecosystems through anthropogenic impacts such as land use, eutrophication, and global warming (Sala 2001, Domisch et al 2013, Weyhenmeyer et al. 2013). Thus an apparent focus has been put on ecosystem functions (EF) and the question whether key functional properties of an ecosystem would be lost with increasingly fewer species to carry out these functions.

Early research on biodiversity (BD) has traditionally considered community composition as BD indicators and how it is regulated by abiotic and biotic constraints with a focus on the maintenance of BD and ecosystem stability aspects (e.g. Hillebrand et al 2007). More recently the emphasis moved to addressing the role of BD on EF- with BD as a driver of EF and vice versa (for review see Hillebrand and Matthiessen 2009). Taxonomic diversity and functional diversity explaining EF (e.g. biomass, productivity, element cycling) dominated the research particularly in terrestrial ecosystems. In this context, the seminal long-term (7 years) grassland experiments by Tilman et al. (2001) were first to show that ecosystem productivity is a function of changes in plant biodiversity. Meanwhile there is cumulative evidence, that the relationship between BD and EF can be transferred to various habitats, trophic levels and ecosystem processes (Worm et al. 2006, Filip et al. 2012). For instance, Ptacnik et al. (2008) have shown that these relationships also apply for phytoplankton communities. By analysing large scale observational data from Scandinavian lakes and from the Baltic Sea for the summer season, they showed that phytoplankton genus richness was positively connected to resource use efficiency for phosphorous across all sites, despite considerable differences in site specific regional diversity and environmental gradients (brackish vs. freshwater; continental vs. oceanic climate), indicating causal effects of phytoplankton diversity and ecosystem functional properties over a large spatial scale. Changes in zooplankton biodiversity or changes in relative species composition has been shown in the context of global warming (for review see Adrian et al. 2009; Wagner & Adrian 2011). Based on decadal data on the physical, chemical and biological limnology of 53 temperate zone lakes in North America and Europe, it was shown that fluctuations in the chemical environment tended to exclude zooplankton species while temperature variability promoted greater richness, indicating an overall neutral net effect (Shurin et al., 2010).

That BD/EF relationships operate bi-directionally (Gamfeld & Hillebrand 2008), has been hypothesized by e.g. Loreau et al. (2001), while the models of Gross and Cardinale (2007) have formalized these hypotheses by showing that resource supply can drive diversity and diversity can drive ecosystem function simultaneously. Hence, changes in environmental forces or diversity are predicted to affect ecosystem function,

especially when ecosystem processes such as primary production are maintained by only a few species (e.g. Vinebrooke et al. 2003).

In Mediterranean lakes climate warming often goes along with an increase in salinity. Diversity pattern along natural salinity gradients are known since long and it becomes increasingly clear that salinity is a major structuring element in aquatic systems, affecting organisms directly and indirectly e.g. zooplankton (Horvath et al. 2013), fish (Bruce et al. 2013) or macroinvertebrate communities (Bruce et al. 2012). A decline in zooplankton diversity has been documented for a number of inland ecosystems (see Horvath et al. 2013 for review).

In the following we provide a number of case studies documenting the role of environmental forces such as temperature, thermal regime, water level, nutrients, salinity on aquatic species composition (plankton, macroinvertebrates, fish), biomass development (plankton, periphyton) and biodiversity (plankton, fish).

### **3. Case studies**

#### **3.1 Case study\_Müggelsee**

##### **Effects of changes in thermal regime on cyanobacteria and copepod community composition and ecosystem function**

**Study site:** Müggelsee (52\_26 ° N, 13\_39 ° E) is a polymictic shallow lake (mean depth 4.9 m, maximum depth 7.9 m) with a surface area of 7.3 km<sup>2</sup>. Since 1980, sampling of plankton and data collection of physical and chemical variables have occurred weekly and, in winter months, biweekly, using standard limnological techniques (Driescher et al., 1993). Mean summer near-surface water temperatures in the lake have shown an increasing trend of about 0.5 °C per decade since 1980 (Adrian et al., 2006). Over the same period, the lake has undergone a change in trophic state from hypertrophic in the 1980s to eutrophic in more recent years (Köhler et al., 2005; Huber et al. 2008).

Wagner & Adrian (2011) studied climate-induced changes in thermal regime in Müggelsee, a shallow polymictic lake, where there has been a 30% increase in the number of summer thermal stratification periods in recent decades (Fig. 1). These stratified periods alternated with intervals of complete mixing, on a temporal scale of 1–8 weeks. They tested for the effects, on a range of community properties, of the increase in the number and length of periods of thermal stratification over a record spanning 26 years (1982–2007). Community properties included species richness, evenness and population size, in addition to the taxonomic composition of the main groups of plankton (cyanobacteria, diatoms, rotifers, cladocerans and cyclopoid copepods), along with changes in ecosystem functioning. They asked how plankton species richness, trait and community composition have been affected by the increase

in the number and extent of periods of summer thermal stratification, in addition to direct temperature effects. Specifically they determine the following: (i) based on annual averages, overall long term trends in community properties during stratified versus mixed periods, (ii) their detailed temporal development in the course of thermally stratified and mixed periods, and (iii) abiotic factors determining community properties, separated for periods of extended thermal stratification and mixing, respectively. The study provides insight into likely consequences of long-term climate change on plankton species composition, diversity, functionality and ecosystem processes operating at short (weeks) and long (decades) temporal scales (Wagner & Adrian 2011).

They found that the overall number of stratification events increased significantly across the study period. When the lake was stratified, consistently higher surface water temperatures and lower epilimnetic nutrient concentrations were found. As the length of thermal stratification increased, the phytoplankton shifted towards a higher proportion of buoyant cyanobacteria capable of N-fixation (*Aphanizomenon*, *Anabaena*), manifested as a change in ecosystem function (Fig. 2). Diatoms were at a disadvantage because of high temperature, exceeding their upper lethal limit and sedimentation losses. Zooplankton species with high thermal tolerances (i.e. *Thermocyclops oithonoides*, *Thermocyclops crassus*) and/or those that grow quickly at high temperatures (i.e. rotifers) became more common. During periods of continuous mixing, the community remained largely unchanged, except for some minor increase in the biomass of diatoms. While a noticeable shift towards N-fixing cyanobacteria was observed with increasing length of stratified events (Fig. 2), and rotifers and copepods became the main predators, there were minimal changes in diversity, except for an increase in cyclopoid copepods and a decrease in diatom diversity. As for cyanobacteria, the net short-term effect on their diversity was neutral as a result of species replacements (Fig. 3). In the long term, however, the diversity of cyanobacteria and cladocerans declined while that of rotifers increased. A detailed description of the study is given in Wagner & Adrian (2011).

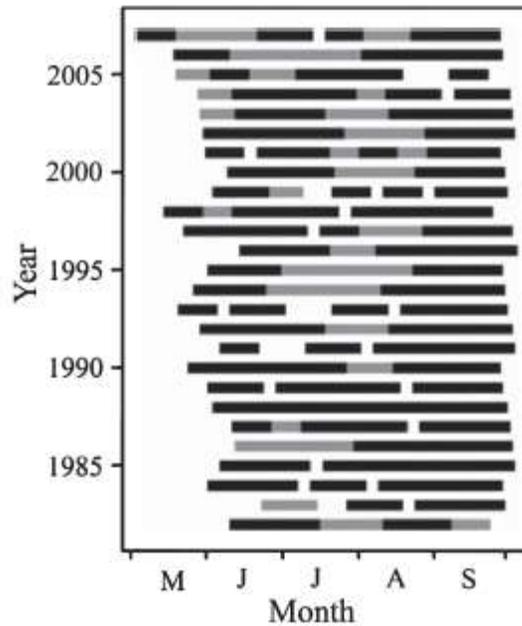


Fig. 1 Thermal regime of Müggelsee during the summer periods between 1982 and 2007. Black bars indicate continuous  $\geq 2$  week periods of mixing; grey bars represent continuous  $\geq 2$  week periods of stable thermal stratification. White intervals represent weeks with opposite mixing status compared to adjacent weeks, i. e., a week with mixing status, that is preceded and followed by a week with stratification (according to Wagner & Adrian 2011). .

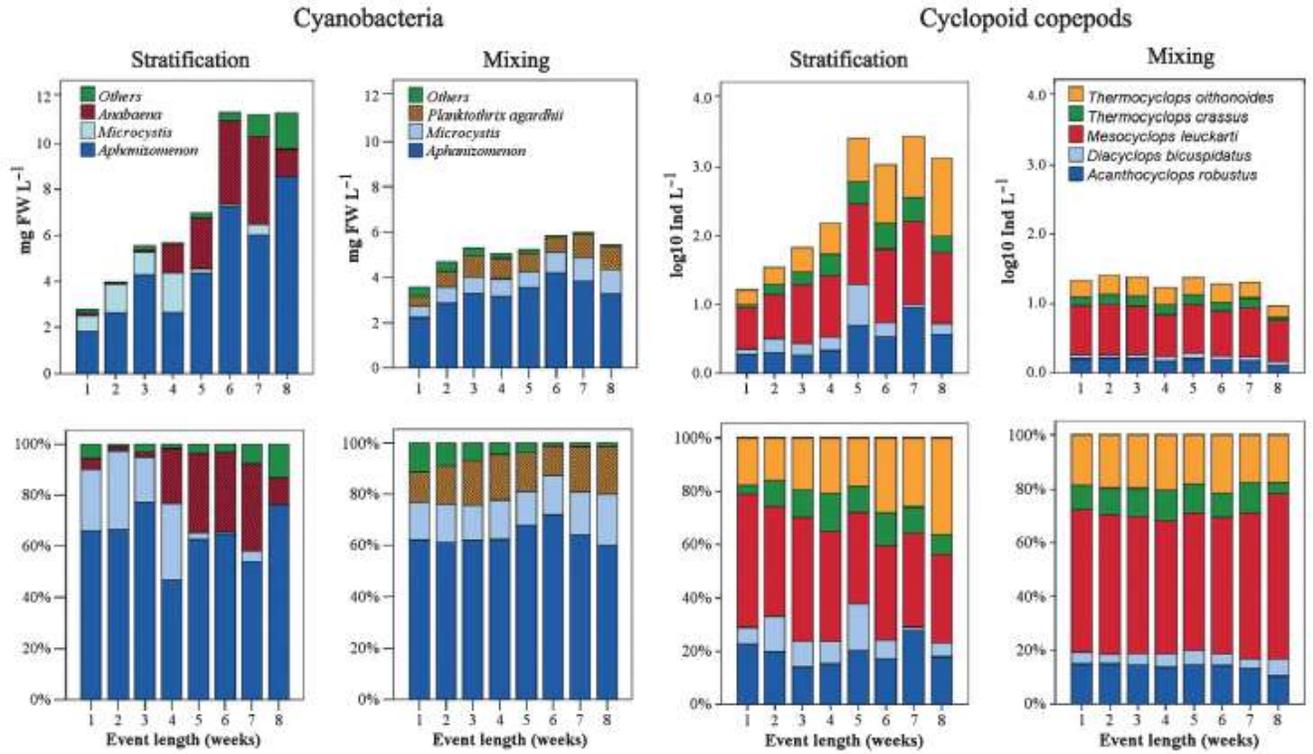


Fig. 2 Taxonomic composition of cyanobacteria (two left-hand columns) and cyclopoid copepods (two right-hand columns) in the course of thermal stratification (columns 1 and 3) and mixing (columns 2 and 4) events between 1 and 8 weeks. The upper row shows the absolute values for cyanobacteria biomass and copepod density; the lower panel shows the respective relative biomass and density. Values for the cyanobacteria genera *Anabaena* and *Plankthotrix* are both striped and coloured in red and orange, respectively, to indicate their particular thermal preference and species replacement. Genera and species, which contributed <5% to the respective biomass and density at any given week, are pooled as 'others' (according to Wagner & Adrian 2011).

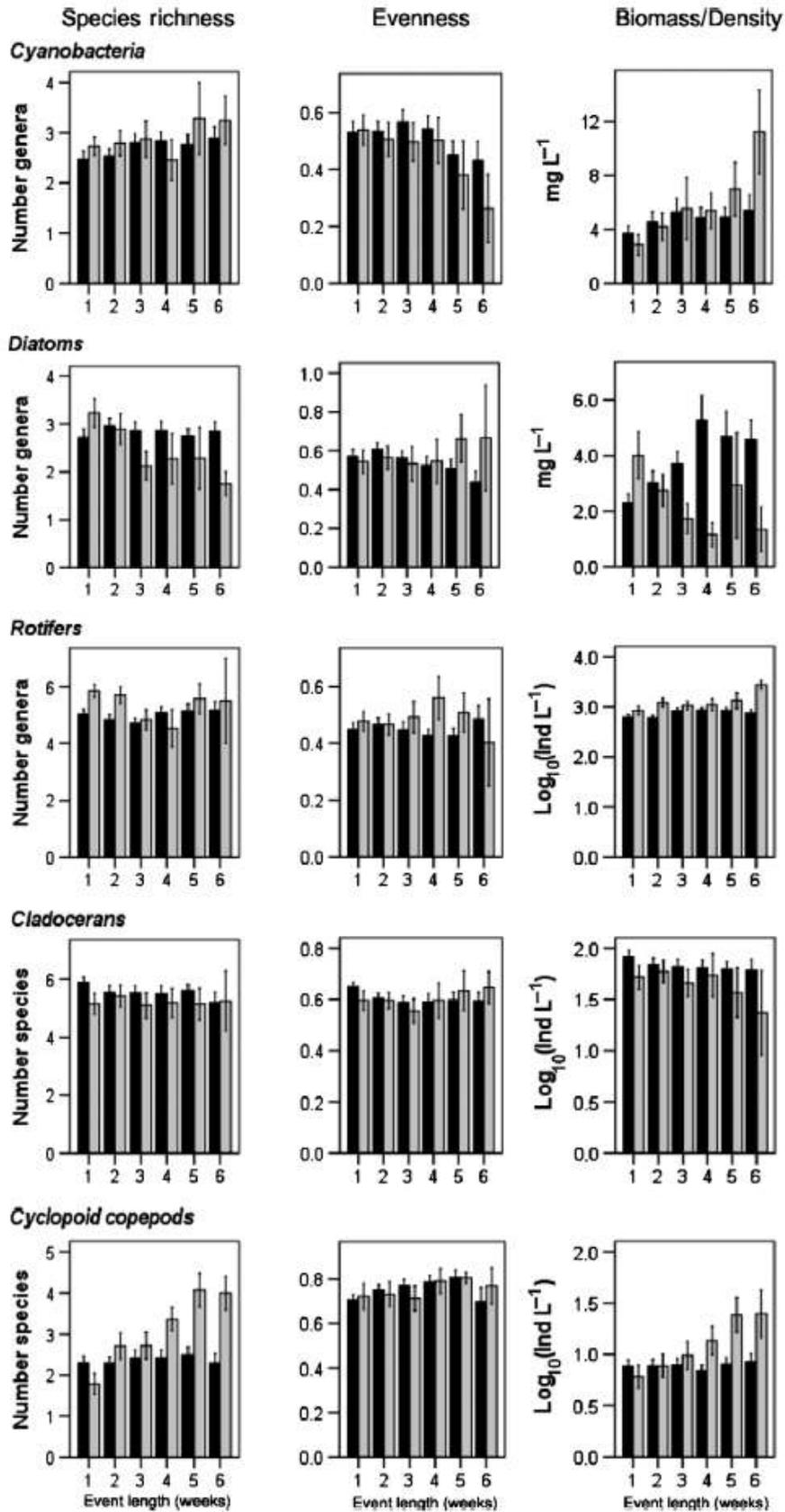


Fig. 3 Community properties of phytoplankton (upper two rows) and zooplankton (bottom three rows) in the course of thermal stratification events (grey bars) vs. mixing events (black bars). Means with standard error bars in the course of events between 1 and 6 weeks for the diversity indices of richness and evenness (columns 1–2) and biomass / density (column 3) ( $\log = \log_{10}$  transformed zooplankton values) are provided. Please note that evenness is a dimensionless index (Wagner & Adrian 2011).

### 3.2. Case study Lake Võrtsjärv

#### Effects of changes in water level on phytoplankton communities

A study of the 44-year data series on Võrtsjärv phytoplankton (Nöges et al., 2010a) suggests a non-linear response of phytoplankton to changing nutrient loadings and the occurrence of a regime shift between 1977 and 1979 triggered by an abrupt water level increase, which supported the establishment of the new highly shade tolerant phytoplankton community dominated by *Limnothrix redekei* and *L. planktonica*.

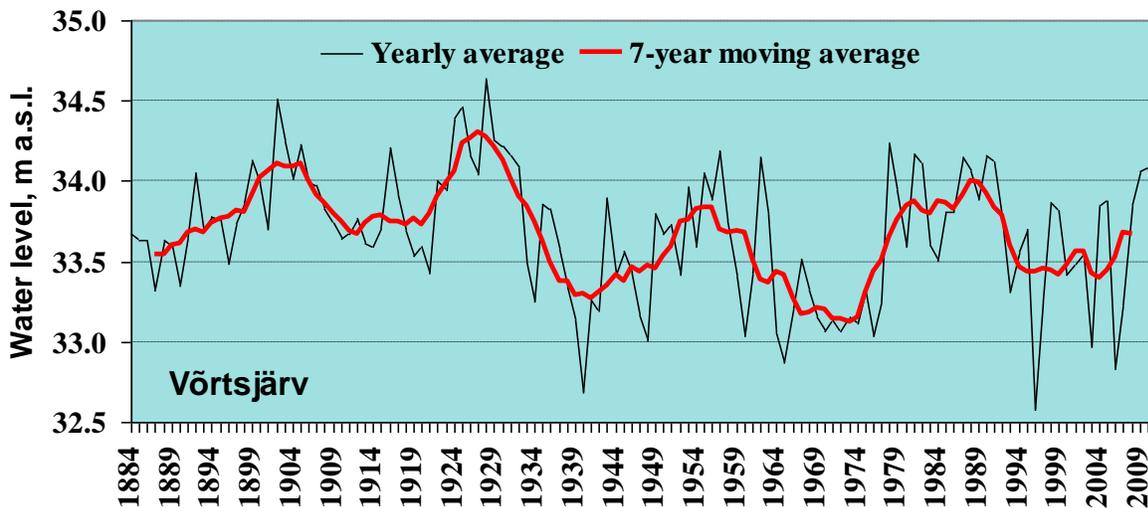


Fig. 4. Long-term changes in the water level of Lake Võrtsjärv

**Study site:** Lake Võrtsjärv is situated in central Estonia and is the second largest lake in the country with a surface area of 270 km<sup>2</sup> and a catchment area of 3,374 km<sup>2</sup>. This very shallow (maximum depth 6 m, mean depth 2.8 m) non-stratified lake has six main inflows and one outflow that carries the water into Lake Peipsi. Owing to its shallowness and large wind-exposed area, the water-body is turbid (Secchi depth ranges from 0.5 to

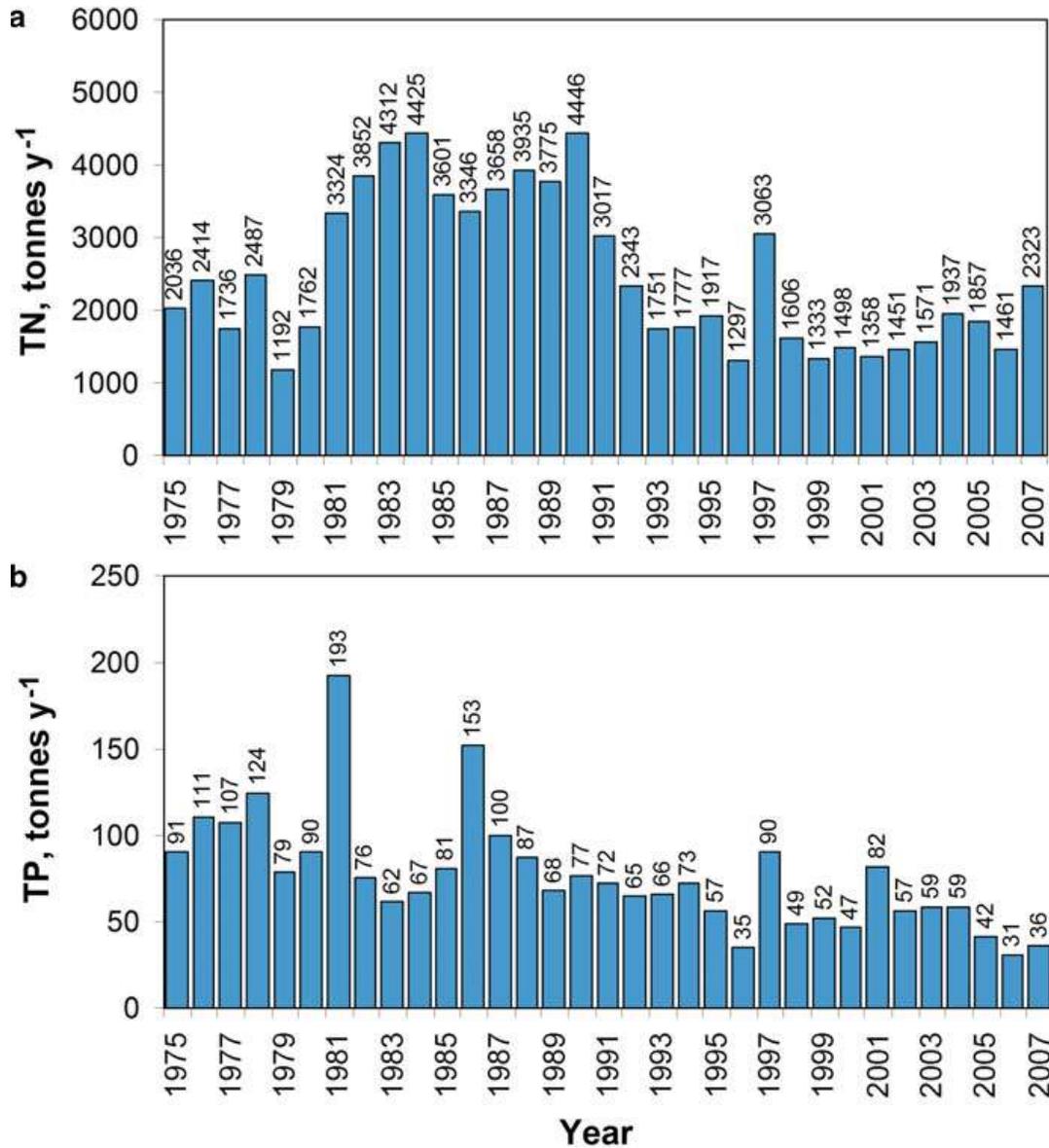


Figure 5. Long-term dynamics of nitrogen (a) and phosphorus loading (b) to Vörtsjärv

1.0 m during the ice-free period). Large natural fluctuation of the water level within a range of 3 metres is the main hydrological peculiarity of the lake affecting growth conditions for phytoplankton. At high water levels, average light conditions in the fully mixed water column deteriorate as the proportion of dark layers increases. This effect is

amplified by the commonly increased humic matter content of water at higher water levels. At low water levels sediment resuspension releases more phosphorus but intensifies denitrification resulting in a drop of the N:P ratio. Besides year-to-year differences, the water level shows a multi-annual periodicity (Fig. 4) well described by the NAO winter index.

The lake is eutrophic, characterised by mean concentrations of about  $1.4 \text{ mg l}^{-1}$  total nitrogen and  $50 \text{ } \mu\text{g l}^{-1}$  total phosphorus. The eutrophication history of Lake Vörtsjärv judged upon changes in carbonate content of sediments along a sediment core shows an increase since the 1950s with a peak during the 1980s (Heinsalu et al., 2008). The 1960s mark the onset of pronounced eutrophication. Measured nutrient loadings since 1975 showed a massive peak in nitrogen loading throughout the 1980s (Fig. 5a) whereas P loadings had a general decreasing trend with still some extremes in the 1980s (Fig. 5b).

With increasing eutrophication pressure, phytoplankton biomass increased and the 1970s can be characterised by highest biomass values for the whole study period since 1964 (Fig. 6), but the phytoplankton composition remained largely the same as described during the first complex expedition in the years 1911-1923 (Mühlen & Schneider, 1920). The dominant species was the cyanobacterium *Planktolyngbya limnetica*, accompanied by diatoms *Aulacoseira ambigua*, *Asterionella formosa* and others. Among green algae, several species of *Pediastrum* were most numerous. Water blooms caused by *Anabaena lemmermannii* in June recurred from year to year until the end of the 1970s.

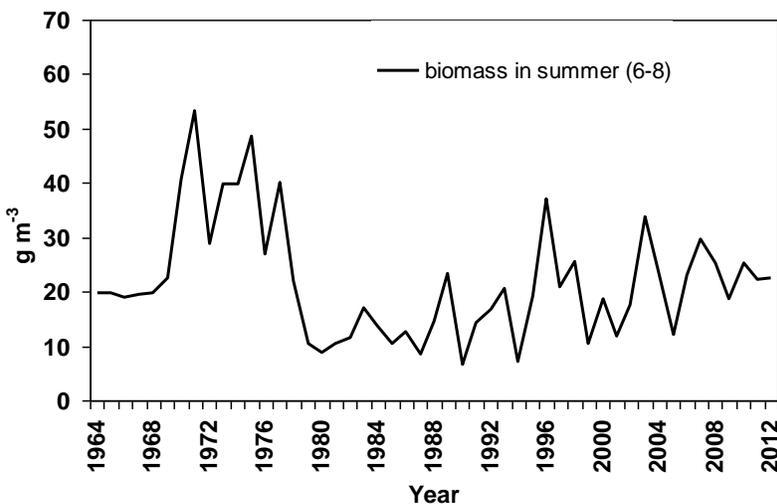


Fig. 6. Long-term changes in summer (June-August) phytoplankton biomass in Vörtsjärv

Sudden change in plankton composition between 1977 and 1979 accompanied by a decrease in the total biomass, involved most of the functional groups and brought about a persistent change in phytoplankton dominant species which replaced *P. limnetica* with highly shade tolerant species. Among several tested phytoplankton indices, the sharp change was best captured by the German PTSI index (Mischke et al., 2008; Fig. 7).

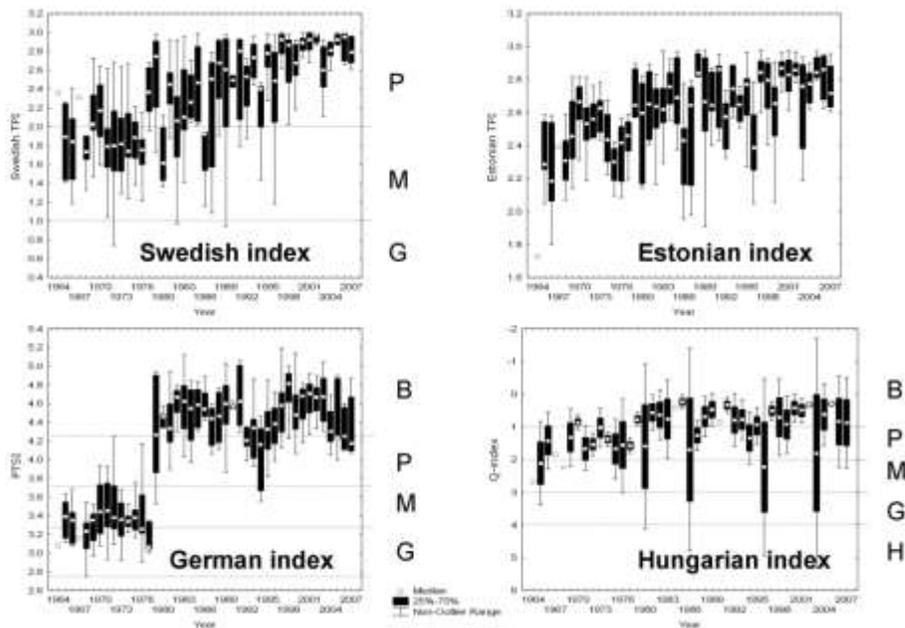


Fig. 7. Long-term changes in ecological status of Vörtsjärv as indicated by some phytoplankton taxonomy based indices: the Swedish index (Willén, 2007), the Estonian index, the German PTSI index (Mischke et al., 2008) and the Hungarian index (Padisák et al., 2006). The full German index is based on three metrics: biomass, algal classes and an indicator taxa based index – PTSI, but here we used only the latter. The status classes H – ‘high’, G – ‘good’, M – ‘moderate’, P – ‘poor’, and B – ‘bad’ are based on WFD normative definitions

Looking for an explanation for the shift around 1978, we first analysed the nutrient pressure. Although heavy loadings over the 1960s and 1970s had obviously destabilised the ecosystem, changes in nutrients could not be the direct initiator of the change as a major increase in both TN and TP loadings occurred only in 1981, i.e. a couple of years after the change in phytoplankton (Fig. 8a). Plotting the PTSI index

against water level changes revealed that the latter was obviously the triggering factor for the change. After a long dry period in the 1960s and most of the 1970s, the extremely rainy summer and autumn of 1978 increased the average water level for the following year by more than a metre. High water level and the increased water colour caused a sharp deterioration of light

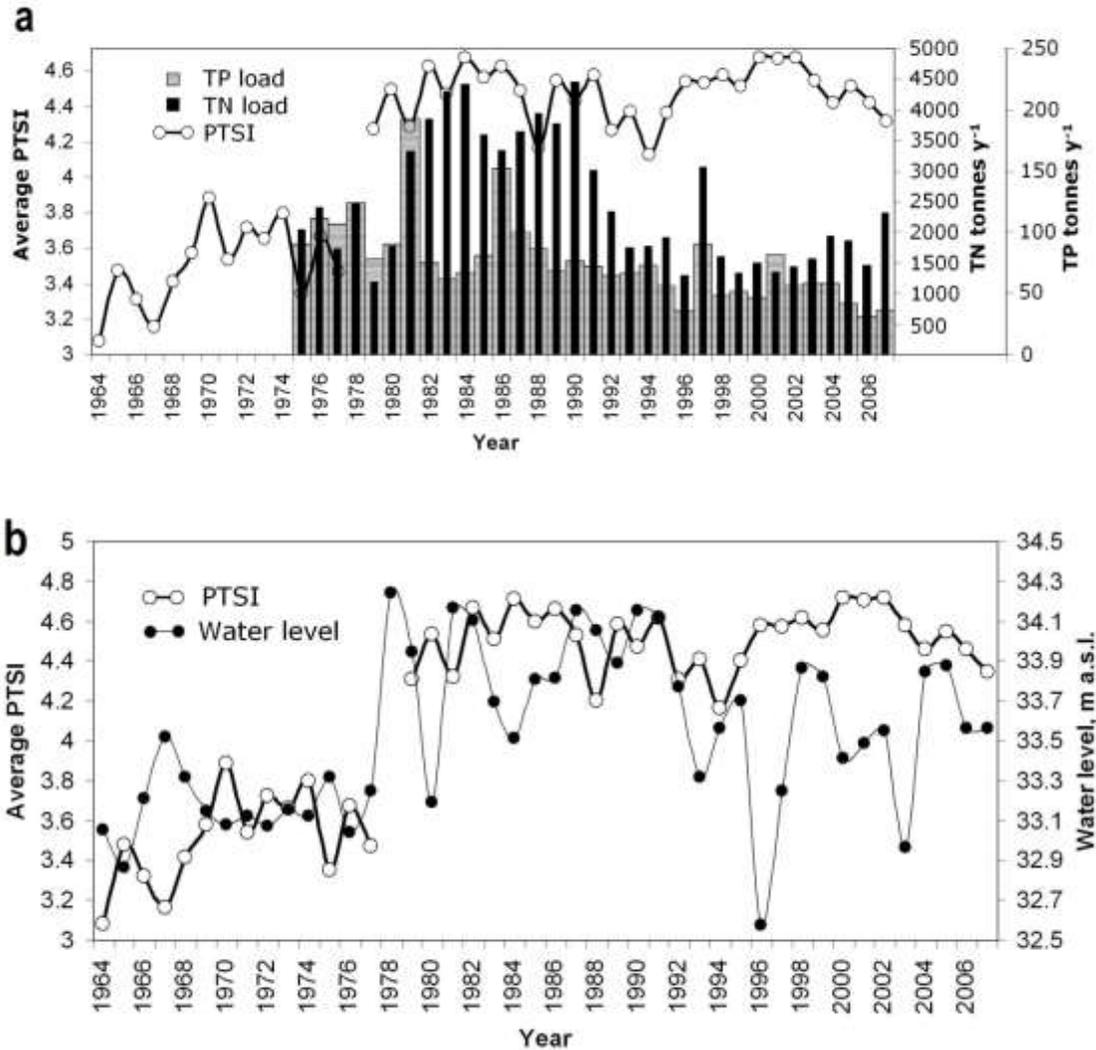


Fig. 8. Long-term changes in the German PTSI index on the background of (a) nutrient loadings to the lake and (b) water level changes.

conditions in the lake and supported the succession of the dominating species. The change was persistent and not reversed by single low water years such as 1996 or 2003. High shade tolerance of the *Limnothrix* species and their efficient use of nutrients for building up biomass (shade) create a self-supporting habitat in which other species

are strongly suppressed. Despite a general and considerable decrease in nutrient loadings, the percentage of filamentous cyanobacteria does not show a decreasing trend. Given the general “browning” trends in many lakes over the northern hemisphere, an increase of humic matter content in Vörtsjärv as a mechanism stabilising the new status over a longer period cannot be excluded. Although we lack direct measurements of dissolved organic matter (DOM) content, the chemical oxygen demand  $\text{COD}_{\text{Mn}}$ , a common proxy for DOM, was significantly lower in the period 1968–1977 compared with that in 1998–2008 and had a highly significant increasing trend within both periods (Tuvikene et al., 2010).

### **3.3. Case study \_Fish diversity across European lakes**

Studies on fish diversity in lakes suggest that there is presumably no single factor that simultaneously predicts diversity, size and density of fish across large spatial gradients. Natural factors and anthropogenic pressures may strongly interact in determining the local fish assemblage in lakes. In the face of the freshwater biodiversity crisis (Dudgeon *et al.*, 2006), it is therefore important to estimate the relative contribution of natural and anthropogenic factors (including climate change) on the macroecological patterns of fish diversity in lakes.

In this study we compiled data from standardized fish monitoring using multi-mesh benthic gill nets and on lake morphometry, and geographical, climatic and anthropogenic pressure variables from 1632 lakes in 11 European countries (Brucet et al. 2013). By means of regression trees we determined those natural and anthropogenic factors and their thresholds that best predicted local fish diversity, density and mean size (Fig. 9).

We found that local fish species richness and diversity were related mainly to morphometric and (bio)geographical/climatic variables. Larger and deeper lakes in warm areas tended to be the most species rich and diverse. Fish density was related mainly to anthropogenically driven productivity but also was sensitive to geographical/climatic factors. Thus, warmer and shallower lower-altitude European lakes, which are usually more eutrophic, had higher fish densities than cold and deeper higher-altitude lakes. Fish size increased with altitude and declined with increasing seasonality and temperature. After controlling for the natural factors, productivity had a positive effect on fish species richness and diversity, whereas it negatively influenced fish size.

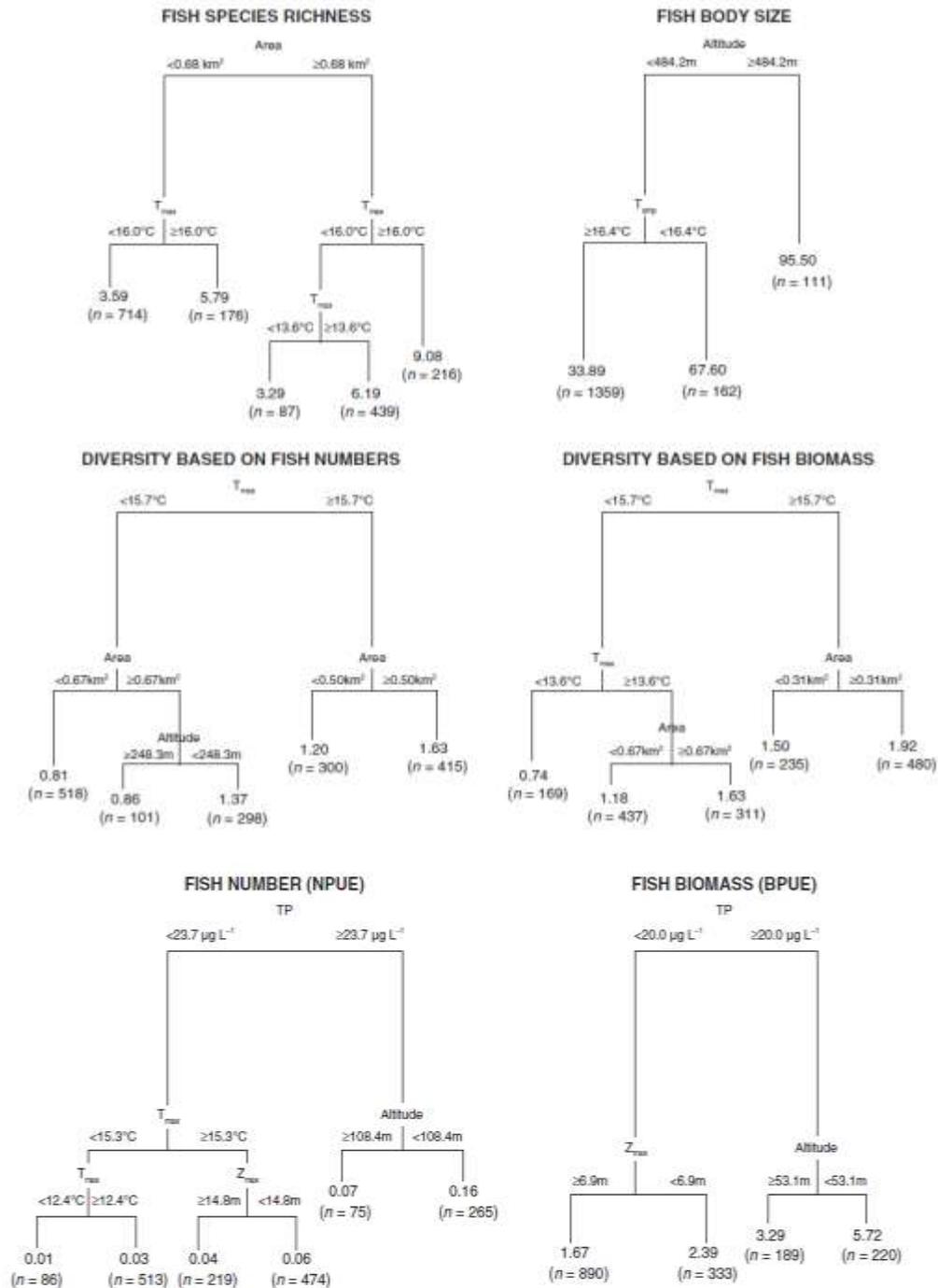


Fig. 9. Regression trees of fish assemblage descriptors for 1632 European lakes. The higher a variable in the tree, the more important it is for differentiating fish assemblage descriptors. Each leaf is labelled with the mean rating and the number of observations in the group (in parentheses). Fish number (NPUE; number fish net m<sup>2</sup> h<sup>-1</sup>), fish biomass (BPUE; g fish net m<sup>2</sup> h<sup>-1</sup>), diversity based on fish number (H<sub>NPUE</sub>), diversity based on fish biomass (H<sub>BPUE</sub>), and body size (BPUE:NPUE ratio; g wet weight). TP (total phosphorus), T<sub>max</sub> (maximum temperature), T<sub>amp</sub> (amplitude of temperature), Z<sub>max</sub> (maximum depth).

Our results suggest that macroecological patterns of lake fish diversity across Europe are best predicted by natural factors. The contribution of anthropogenic factors to fish diversity was evident only via the effect of eutrophication at smaller geographical scales, whereas no effect could be found from hydromorphological pressures. From an applied perspective, these results suggest that bioassessment and biodiversity evaluation might be most effectively conducted and interpreted locally, where anthropogenic effects on biodiversity become more visible. At a macroecological scale, our results also suggest that temperature differences, mainly related to geographical gradients and lake morphometry, strongly predict most components of fish diversity, emphasizing the importance of temperature in determining broad-scale patterns of fish diversity in European lakes. Therefore, subtle changes of fish diversity in lakes may be early indicators of the effects of global warming, a process that presumably has only started to become visible (Fig. 10).

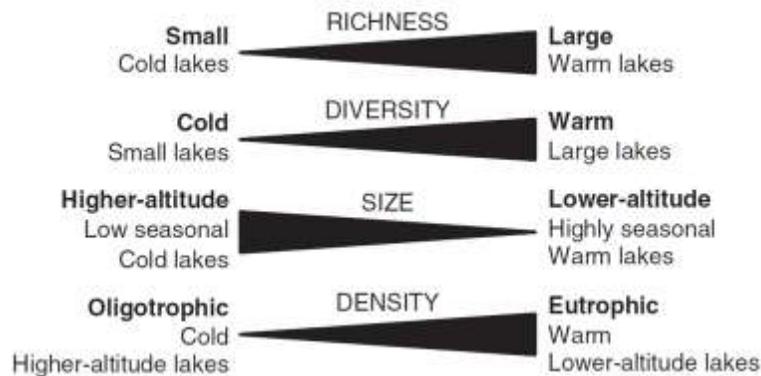


Fig. 10. Scheme showing changes (increase and decrease) for each fish assemblage descriptor in European lakes. Main variables driving changes in each descriptor are given in bold.

### 3.4. Case study \_ Macroinvertebrate diversity across two climatic regions

Climate warming may lead to changes in the trophic structure and diversity of shallow lakes as a combined effect of increased temperature and salinity and likely increased strength of trophic interactions. We investigated the potential effects of temperature, salinity and fish on the plant-associated macroinvertebrate community structure and biodiversity by introducing artificial plants in eight comparable shallow brackish lakes located in two climatic regions of contrasting temperature: cold-temperate and

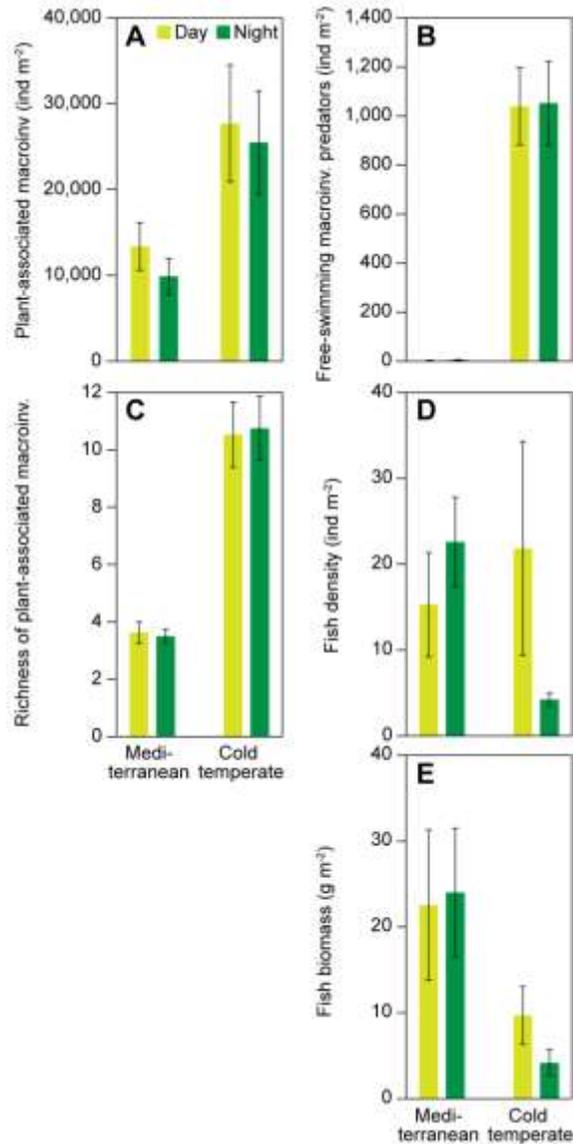


Fig. 11. Densities of plant-associated macroinvertebrates, free-swimming potentially predatory macroinvertebrates and fish, and taxon richness of plant-associated macroinvertebrates. The data are means ( $\pm 1$ SE) of data collected at day and night-time in four lakes in the cold temperate region and four lakes in the Mediterranean region. Fish biomass in fresh weight.

Mediterranean (Brucet et al 2012). In both regions, lakes covered a salinity gradient from freshwater to oligohaline waters. We undertook day and night-time sampling of

macroinvertebrates associated with the artificial plants and fish and free-swimming macroinvertebrate predators within artificial plants and in pelagic areas.

Our results showed marked differences in the trophic structure between cold and warm shallow lakes. Plant-associated macroinvertebrates and free-swimming macroinvertebrate predators were more abundant and the communities richer in species in the cold compared to the warm climate, most probably as a result of differences in fish predation pressure (Fig. 11).

The richness and abundance of most plant-associated macroinvertebrate taxa decreased with salinity.

Submerged plants in warm brackish lakes did not seem to counteract the effect of fish predation on macroinvertebrates to the same extent as in temperate freshwater lakes, since small fish were abundant and tended to aggregate within the macrophytes. Despite the lower densities of plant-associated macroinvertebrates in the Mediterranean lakes, periphyton biomass was lower than in cold temperate systems, a fact that was mainly attributed to grazing and disturbance by fish (Fig. 11).

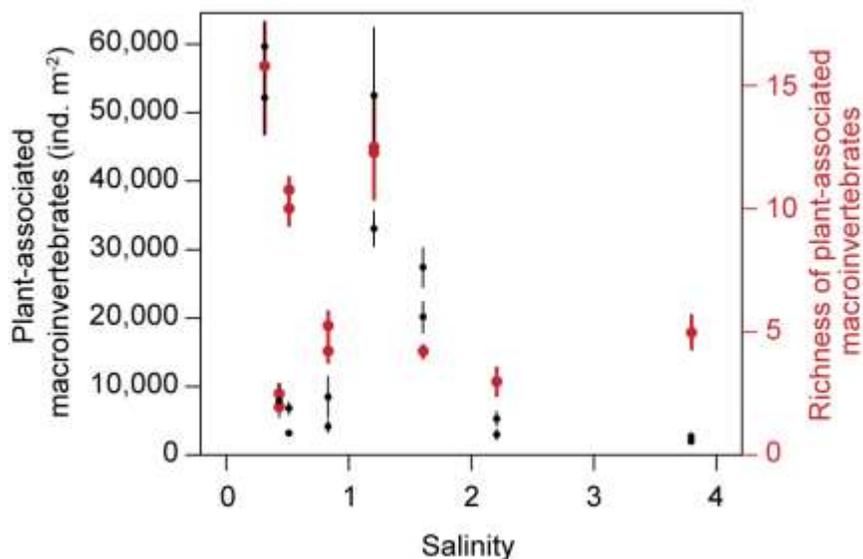


Fig. 12. Plant-associated macroinvertebrates along the salinity gradient. Plant-associated macroinvertebrates density in black and richness in red ( $\pm 1SE$ ).

Our results suggest that, if the current process of warming entails higher chances of shallow lakes becoming warmer and more saline, climatic change may result in a decrease in macroinvertebrate species richness and abundance in shallow lakes. Some

brackish and saline lagoons might be capable of coping with slight increases in salinity since the organisms dominating these systems can tolerate varying salinities, and well-structured communities can be found at high salinities. However, as has been suggested for zooplankton, rising salinity levels, together with increasing temperatures, could have dramatic effects in slightly brackish waters (<5), whose macroinvertebrate communities comprise species from saline and freshwaters, and even more severe impacts on current freshwater lakes (Fig. 12).

### **3.5. Case\_study Periphyton development in lakes across a north/south European geographical gradient**

Periphyton communities play an important role in shallow lakes and are controlled by direct forces such as temperature, light, nutrients and invertebrate predation, but also indirectly by fish predation. In REFRESH we performed a pan-European lakes mesocosm experiment on periphyton colonization covering 5 countries along a north/south geographical/temperature gradient (Estonia, Germany, Czech Republic, Turkey, and Greece). For details on the sites see Table 1 (Mahdy et al. in preparation).

We studied periphyton development in mesocosms with two different nutrient loadings and a moderate fish density in five European countries for a one month period in July/August 2011. Periphyton biomass was colonized on artificial strips exposed at 50 cm mesocosm water depth under low ( $25 \mu\text{g TP L}^{-1}$ ) and high ( $200 \mu\text{g TP L}^{-1}$ ) nutrient regimes during mid-summer. Even though our nutrient loading (TP) was implanted, there was no significant effect on periphyton biomass. Water temperature played an important positive role on summer periphyton biomass development. The slope of the regression between water temperature and periphyton biomass suggested that, for every degree increase in water temperature, summer periphyton biomass was stimulated by 42% (Figure 13).

Table 1 Lake mesocosm experiment: Basic information, modified from Landkildehus et al., submitted).

<b>Experimental site</b>	<b>Coordinates</b>	<b>Climate</b>	<b>Altitude (m a.s.l)</b>	<b>No. meso- cosm</b>	<b>Total precipi- tation (mm)</b>	<b>Mean air temperat ure (°C)</b>
Czech Republic, Vodňany	49°09'14"N, 14°10'11"E	Transient maritime/ Continental	395	8	401	15.3
Germany, Müggelsee	52°26'0" N 13°39'0" E	Transient maritime/ Continental	32.4	5	431	16.9
Estonia, Võrtsjärv	58°12'17" N 26°06'16" E	Boreal	35	8	298	14.4
Turkey, ODTU-DSI Golet	39°52'38" N 32°46'32" E	Transient /continental Mediterranean	998	8	223	18.8
Greece, Lysimachia	38°33'40" N 21°22'10" E	Mediterranean	16	8	252	23.9

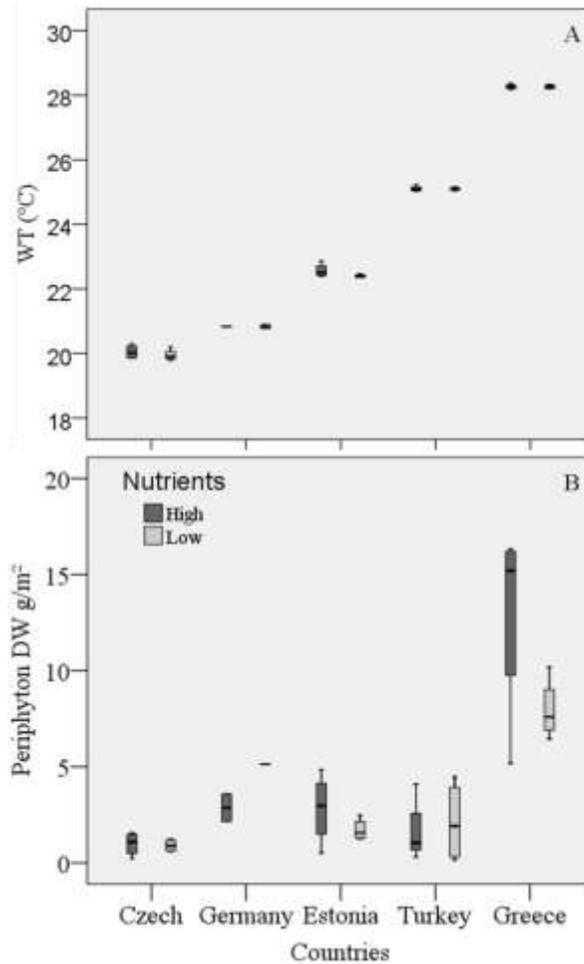


Fig. 13. Mean (A) water temperature (WT) and (B) periphyton dry weight (DW) in mesocosm experiments in five European countries with two nutrient scenarios (high and low).

A positive top-down effect by fish on periphyton biomass was detected due to a control of periphyton scraping invertebrates grazers. The slope of the regression between fish biomass and periphyton chl *a* adjusted to water temperature suggested that, for every degree increase in water temperature and its equivalent top-down control of invertebrate grazers by fish, summer periphyton biomass (chl *a*) was stimulated by 45%. The study suggested that care should be taken when predicting the combined effect of changes in multiple factors from their individual effects.

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