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Abstract

This deliverable presents results from work undertaken on three shallow, eutrophic and frequently mixing European lakes, Säkylän Pyhäjärvi (Finland), Võrtsjärvi (Estonia) and Müggelsee (Germany). These were analysed to determine the importance of stratification and mixing episodes (thermal stability) in shaping the nutrient and oxygen concentrations in the water column, and the abundance and diversity of phyto- and zooplankton during summer. The results were obtained by analyzing high-frequency monitoring data for water temperature, dissolved oxygen, chlorophyll *a* and biomass of cyanobacteria, weekly to monthly data on inorganic and total nutrients, and the phytoplankton and zooplankton composition in June-August 2008-2011.

The thermal regimes of the study lakes were characterized by low water column stability and short stratification periods of 1-34 days in duration followed by a partial or complete mixing of the water column. During stratification, the partitioning of the concentrations of oxygen, inorganic nutrients (phosphorus and nitrogen) and iron (Fe) increased between the epi- and hypolimnion. Chlorophyll *a* and phytoplankton biomass were higher during mixing episodes/weak stratification in Pyhäjärvi and Võrtsjärvi. Increased mixing lead to a higher biomass of centric diatoms, but in Pyhäjärvi cyanobacteria were also favoured by the breakdown of stratification. Phyto- and zooplankton diversity (taxa richness, H', Evenness) were not clearly affected by different thermal regimes of the study period. The results show that shallow lakes can react rapidly to changing thermal regime and therefore their nutrient dynamics and functional traits of plankton are sensitive to temperature-induced changes.

1 **Manuscript**

2

3 Mixing induced changes in nutrients and plankton in shallow European lakes

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23 This paper has not been submitted elsewhere in identical or similar form, nor will it be during the
24 first three months after its submission.

25

26 **Abstract**

27 Effects of stratification and mixing events on the concentrations of nutrients, and the abundance and
28 diversity of phyto- and zooplankton during summer were studied in three shallow polymictic lakes
29 in Northern and Central Europe using frequent data on water temperature, dissolved oxygen,
30 chlorophyll *a* and biomass of cyanobacteria, and weekly to monthly data on inorganic and total
31 nutrients, and phytoplankton and zooplankton composition. During 2008-2011 the thermal regime
32 of lakes in June-August was characterized by low water column stability (Schmidt stability of <3.5
33 J m^{-2}) and short stratification periods of 1-34 days in duration followed by a partial or complete
34 mixing of the water column. During stratification, the contrasts of the concentrations of oxygen,
35 inorganic nutrients (phosphorus and nitrogen) and iron increased between epi- and hypolimnion.
36 Concentrations of chlorophyll *a* and the phytoplankton biomass were higher during mixing
37 episodes. Changes in mixing also affected phytoplankton species composition with e.g. more
38 centric diatoms during mixing. Phyto- and zooplankton diversity (taxa richness, H' , evenness) were
39 not clearly influenced by different mixing or stratification episodes. The results show that shallow
40 polymictic lakes can react rapidly to changing thermal regime and therefore their nutrient dynamics
41 and functional traits of plankton are sensitive to temperature-induced changes.

42

43

44 **Keywords**

45 mixing, thermal stratification, stability, phytoplankton, zooplankton, plankton diversity, lakes,
46 climate change

47

48 **Introduction**

49

50 Climate change with increased air temperatures and changes in cloud cover, radiation and wind
51 speed affect the heat content and stratification of lakes (Saloranta et al. 2009, Arvola et al. 2010,
52 Jones et al. 2010, Forsius et al. 2010). Water temperature changes have direct effects on the
53 chemical and biological processes in the water column and sediments, e.g. by affecting growth
54 rates, metabolism and microbial processes (e.g. Montagnes et al. 2008, Pettersson et al. 2010). In
55 turn, indirect temperature effects on lakes occur largely via changes in stratification and mixing, the
56 key factors of lake ecosystems that affect oxygen conditions, and nutrient recycling in the water
57 column (Forsius et al. 2010) and the distribution, abundance and composition of plankton
58 (Reynolds 2002, Nõges et al. 2010, Wagner & Adrian 2011). During summer and autumn,
59 intermittent partial or complete breaking of stratification increases mixing and upwelling of
60 nutrients to the epilimnion, and the extent of ecosystem response typically depends on how long
61 mixing continues or a new stratification period prevails. The upwelling of nutrient-rich waters in
62 lakes is often followed by phytoplankton blooms, largely diatoms (e.g. Willén 1991, Wilhelm &
63 Adrian 2008).

64

65 Response to meteorological forcing differs between the lakes depending on their morphometry,
66 trophic state, water colour and geographic location (Snucins & Gunn 2000, Gerten & Adrian 2001,
67 2002, Houser 2006, Saloranta et al. 2009, Jones et al. 2010). For instance, in deep dimictic lakes
68 temperature induced changes in thermal characteristics (e.g. in hypolimnetic water temperatures)
69 are discernible over long periods whereas in shallow and frequently mixing polymictic lakes the
70 temperature induced signal may disappear rapidly (Gerten & Adrian 2002, Arvola et al. 2010).
71 Similarly the species-specific responses among planktonic taxa to changes in stratification/mixing
72 regime are diverse. In eutrophic lakes, prolongation of thermal stratification has typically lead to
73 higher proportions of cyanobacteria, lower proportions of cold water preferring and mixing
74 sensitive diatoms, and to zooplankton composition with species which have high thermal tolerances
75 (e.g. the copepods of the genus *Thermocyclops*) or which can grow fast at high temperatures, e.g.
76 the rotifers (Paerl & Huisman 2008, Wagner & Adrian 2009, 2011, Kosten et al. 2012). Changes in
77 zooplankton biomass and species composition in the pelagial of shallow lakes are often related to
78 trophic state, rather than to summer climate (Gyllström et al. 2005). However, strong temperature
79 rises during extended thermally stratified events showed a significant correlation with the increase
80 in thermophilic copepod species on small temporal scales (Wagner and Adrian 2011). Shurin et al.
81 (2010) nicely disentangled variability in temperature versus nutrients affecting zooplankton

82 diversity. Their results suggested that temporal fluctuations in the chemical environment tend to
83 exclude zooplankton species while temperature variability promotes greater richness. The results
84 indicated that anthropogenic increases in temporal variability of future climate may have profound
85 effects on biodiversity.

86

87 It has been experimentally shown that environmental variability at intermediate scales of 20-200
88 hours tend to preserve species diversity of phytoplankton, while higher frequencies of disturbance
89 lead to decreases in phytoplankton diversity (Reynolds 1988, Flöder & Sommer 1999). Also,
90 modeling of mixing processes has suggested that turbulent mixing is a major determinant of the
91 species composition of phytoplankton blooms. In well mixed environments the species with low
92 critical light intensity should dominate whereas during stratification they should be replaced by
93 species that can better adjust their position in relation to light gradient (Huisman et al. 1999).
94 Analysis of long time-series from the German polymictic lake Müggelsee suggest that the climate
95 induced changes in thermal regime may affect more the relative composition of phyto- and
96 zooplankton and key functional traits (e.g. N-fixation), but have less influence on the total diversity
97 (Wagner & Adrian 2011). Phytoplankton compositional responses to changes in mixing can also be
98 considered in terms of functional groups (Reynolds 1988, Reynolds et al., 2002, Padisák et al.
99 2009). Wilhelm and Adrian (2008) showed that in a shallow and eutrophic Müggelsee the
100 functional groups C (vernal diatoms, e.g. *Stephanodiscus*) and X2 (eutrophic nanoplankton, e.g.
101 *Chrysochromulina*) correlated significantly with the depth of thermocline or with the stratification
102 intensity.

103

104 Here we present results of the effects of changes in mixing and stratification on nutrient
105 concentrations and plankton abundance and diversity in three shallow, eutrophic and polymictic
106 lakes located in different regions of Europe (Finland, Estonia and Germany). In the analysis we use
107 water column stability, derived from high-frequency water temperature monitoring, as a proxy for
108 stratified and mixed periods and focus on the stability effects on phosphorus and nitrogen
109 concentrations, the abundance and biomass of phyto- and zooplankton, and plankton diversity
110 (species richness, diversity and community composition) during summer.

111

112 **Methods**

113 Study sites

114 The study sites represent shallow polymictic lakes located in Northern and Central Europe (Table
115 1). Müggelsee (SE Berlin, Germany) is a eutrophic lake that has a short retention time (25-28 weeks

116 in June-August, Wilhelm & Adrian 2008). The lake has been intensive studied for a long time for
117 the ecosystem responses to climate change (e.g. Adrian et al. 1999, Gerten & Adrian 2001, Wilhelm
118 & Adrian 2008, Wagner & Adrian 2009, 2011). A more comprehensive limnological
119 characterization of the lake is presented in Driescher et al. (1993). L. Võrtsjärv (Estonia) is the
120 second largest lake in the Baltic countries and the largest domestic water body in Estonia. In most
121 areas of the lake the depth is less than 3 m. Ecosystem of the lake is strongly affected by
122 fluctuations in water level (Nõges et al. 2003). As for Müggelsee the ecosystem responses of L.
123 Võrtsjärv to the climate-related variation have been widely studied (see e.g. references in Nõges et
124 al. 2010). L. Pyhäjärvi (SW Finland) is a large and shallow lake suffering from eutrophication. The
125 lake has been intensively studied for decades and it has been the object of restoration activities for
126 >20 years (Ventelä et al. 2011). The biggest concerns with the status of Pyhäjärvi are related to
127 external nutrient loads and how they are influenced by the changing climate.

128

129 Data:

130 The study is largely based on the analysis of high-frequency (hourly-daily-weekly) monitoring data
131 from June-August 2008-2011. For Müggelsee, profiles of water temperature and oxygen were
132 measured weekly from the depth of 0-7.5 m at 0.5 m intervals. Chemical data were collected
133 weekly during stratification from integrated samples representing the upper water layer (0.5-3.5 m;
134 epilimnion) and the lower water layer (4.5-7.0 m, hypolimnion), and during the mixing periods
135 from the whole water column (0-7.0 m). The separation of the upper and lower water layers during
136 the stratified period does not always correspond to the epilimnion and hypolimnion as determined
137 by the thermocline depth (Wilhelm & Adrian 2008). Phytoplankton samples were taken as
138 integrated samples from the epilimnion (0-3.5 m), and the composite zooplankton samples
139 integrating the whole water column.

140

141 For Võrtsjärv, daily temperature profiles were measured in 2009-2011 from the surface (0.5-1.0 m)
142 to the depth of 4 m at 0.5-1.0 m intervals. Oxygen and chlorophyll *a* concentrations were measured
143 daily from the depth of 0.5-1.0 m. Cyanobacterial abundance was recorded daily in late summer-
144 autumn 2009 and throughout the summer in 2010 using a YSI 6131 sensor, which measures the
145 fluorescence in phycocyanin. The results were converted to cyanobacterial cells numbers (ml^{-1}) by
146 calibration with counted samples. Since L. Võrtsjärv is shallow and usually well mixed, water
147 chemistry has only been monitored monthly from the integrated 2-L samples mixed from the depths
148 of 0.5 m, 1 m, 2 m, and up to the depth of 6 m, depending on water level. Integrated phyto- and

149 zooplankton composition samples, representing the uppermost 4 m of the water column, have been
 150 taken monthly.

151

152 For Pyhäjärvi, vertical profiles of water temperature and oxygen (Marvet sensors) have been
 153 recorded hourly from the deepest part of the lake at the depths of 1.5, 5, 10, 15 and 19 m in 2008
 154 (August 19th-), and in 2009 from the depths of 5, 10 and 19 m (May-October). Turbidity (S::can
 155 Nitro::lyser, spectral 200-700 nm), chlorophyll *a* and the biomass of cyanobacteria (Trios Micro Flu
 156 chlorophyll fluorescence at 470/685 nm, Trios Micro Flu blue fluorescence at 625/655 nm,
 157 respectively) have been recorded hourly during the same periods at the depth of 1 m. In 2010-2011
 158 the automatic measuring station of Pyhäjärvi located close to the River Yläneenjoki sub-catchment
 159 in the shallow southern part of the lake. Data from these years were excluded from the analysis
 160 because of the shallowness of the site, and the fact that water chemistry and plankton data have
 161 been collected in the deepest part of the lake located several kilometers apart. Water chemistry data
 162 was collected from the depths of 1, 5, 10, 15, 20 and 24 m in 2008 and in 2009-2011 from the
 163 depths of 1, 15 and 24 m. The results from the depths of 0-5 and 15-24 m were averaged to
 164 represent epi- and hypolimnion, respectively. Phytoplankton data has been collected biweekly to
 165 monthly from the deepest part of the lake. In the study the phytoplankton results of both SYKE (0-2
 166 m integrated samples) and the Pyhäjärvi Institute (0-5 m integrated samples) were used.

167 Comparison of results of eight phytoplankton samples taken during the same day by both institutes
 168 showed that the results of phytoplankton total biomass and composition do not differ ($p > 0.5$,
 169 Wilcoxon paired-sample test), and for those days the results from the both analysis were averaged.

170

171 Soluble reactive phosphorus (SRP), total phosphorus (TP), nitrate- (NO_3^- -N) or nitrite+nitrate-
 172 nitrogen ($\text{NO}_2^- + \text{NO}_3^-$ -N), total nitrogen (TN) and iron (Fe) were analyzed using standard methods
 173 (e.g. APHA, 2000). Stability of the water column was estimated by calculating the Schmidt stability
 174 (J m^{-2}) from the daily/weekly water temperature profiles. The stratification periods were
 175 distinguished to represent weak stratification and/or mixing periods by using the stability criterion
 176 of $> 3.5 \text{ J m}^{-2}$, which corresponded well with the water temperature difference exceeding 1°C
 177 between the surface and the deeper water layers (Müggelsee 0-1 m vs. 5.0 m, Vörtsjärv 0-1m vs. 4.0
 178 m and Pyhäjärvi 5m vs. 19 m) (Table 2). The temperature difference criterium of 1°C between the
 179 surface and deep water layers has earlier been used to define stratification of L. Müggelsee by
 180 Wilhelm and Adrian (2008). In our study the difference in temperature was $> 1^\circ\text{C}$ only in four
 181 cases when the stability was $\leq 3.5 \text{ J m}^{-2}$.

182

183 Quantitative phyto- and zooplankton composition data was used to estimate effects of stratification
184 and mixing on the diversity of plankton by using the following parameters: the Shannon-Wiener
185 diversity index (H') calculated from biomass (for phytoplankton) and from abundance (for
186 zooplankton), Evenness, the total number of taxa, and the number of taxa of selected phytoplankton
187 groups. Number of taxa was estimated using species data for phytoplankton and genus level data for
188 zooplankton using. In all the studied lakes plankton counting and identification has been carried out
189 using harmonized methods which guarantees the comparability of results between different years
190 (e.g. CEN 15204, 2006).

191

192 Statistical analyses

193 Nonparametric Mann-Whitney U was used to test differences in water chemistry and plankton
194 community properties between stratified and non-/weakly stratified periods, and for the
195 phytoplankton samples of L. Säkylän Pyhäjärvi taken by SYKE and the Pyhäjärvi Institute at the
196 same time. Relationships between water stability, and water chemistry and properties of plankton
197 were studied using Spearman correlation analysis.

198

199 **Results**

200

201 The lakes were mostly mixing or had a weak stratification ($\leq 3.5 \text{ J m}^{-2}$) during June-August in 2008-
202 2011 (Fig. 1). The periods of stratification, with a Schmidt stability of $> 3.5 \text{ J m}^{-2}$, were found in
203 Müggelsee on 37 days (38 % of the study period), in Vörtsjärv only on 6 days (3 %) and in
204 Pyhäjärvi on 36 days (52 %; summer 2009) (Table 2). The strength of stratification was rather low
205 ($3.5\text{-}62 \text{ J m}^{-2}$) also during the stratified periods and the duration of stratification lasted typically less
206 than one week (1-34 days) (Fig. 2, Table 3).

207

208 For physical and chemical properties, the stratified periods were characterized by higher surface
209 water temperature, and for Müggelsee also by higher $\text{NO}_3+\text{NO}_2\text{-N}$ concentrations in the epilimnion
210 compared to the periods of weak stratification/mixing (Table 3). During the stratified periods, the
211 hypolimnetic oxygen concentrations were lower, whereas the concentrations of inorganic P and N
212 fractions (SRP, $\text{NH}_4\text{-N}$, $\text{NO}_3+\text{NO}_2\text{-N}$), total P, and Fe were higher in Pyhäjärvi and Müggelsee than
213 during the mixing periods (Mann-Whitney U test, $p < 0.05$). For Vörtsjärv, the differences between
214 epi- and hypolimnion could not be studied due to integrated water samples that did not separate the
215 two water layers.

216

217 Chlorophyll *a* concentrations and the total biomass of phytoplankton increased during mixing
 218 periods in Pyhäjärvi, while in Müggelsee and Vörtsjärv the difference could be found only for
 219 chlorophyll *a*. Effects of different stratification and mixing events on phytoplankton composition
 220 were discernible foremost at the order and/or class level, while no clear differences were found in
 221 the diversity properties (taxa richness, Shannon diversity index and Evenness) (Table 4). During
 222 mixing enhanced biomass of cyanobacteria and diatoms was observed. As for diatoms the increase
 223 was larger for centric diatoms (order Eupodiscales). We found negative relationship between
 224 stability and total biomass of cyanobacteria in Pyhäjärvi in May-October 2009 (Figure 3). There the
 225 breakdown of stratification was followed almost immediate by the increase in cyanobacteria, and
 226 the stability and cyanobacteria followed each other as mirror images throughout the season.

227
 228 Typically one to seven phytoplankton taxa contributed >5% to the total phytoplankton biomass both
 229 during stratified and non-stratified periods (Table 4). For Müggelsee, the taxa that generally
 230 contributed >5% to total biomass of phytoplankton during the stratified periods were: the
 231 cyanobacteria *Aphanizomenon flos-aquae*, several *Anabaena* species (*A. flos-aquae*, *A. circinalis*, *A.*
 232 *crassa*, *A. smithii*), *Planktothrix agardhii* and *Microcystis* spp., the diatoms *Aulacoseira granulata*,
 233 small centric diatoms and *Diatoma tenuis*, the dinoflagellates *Peridinium* spp. and *Kolkwitzella*
 234 *acuta*, and the cryptomonads *Cryptomonas* and *Plagioselmis*. Chlorophyte taxa (*Oocystis*,
 235 *Pediastrum boryanum*, *P. duplex*, *Phacotus lenticularis*, *Closterium* and *Mougeotia*) and the
 236 prymnesiophyte *Chrysochromulina* had a larger biomass contribution to the total biomass
 237 occasionally, typically only at individual time periods. During mixing episodes, the dominant taxa
 238 in Müggelsee were largely the same: *Aphanizomenon flos-aquae*, *Anabaena flos-aquae*, *A. crassa*,
 239 *Anabaena* sp., *Microcystis* spp., *Aulacoseira granulata*, small centric diatoms, *Diatoma tenuis*,
 240 *Peridinium* spp., *Ceratium* spp., *Kolkwitzella acuta*, *Cryptomonas* and *Plagioselmis*.

241
 242 For Vörtsjärv, phytoplankton composition data was only available from the mixing periods, and
 243 then the biomass was dominated (>5% of total biomass in the sample) by many taxa preferring
 244 turbulent conditions: the cyanobacteria *Aphanizomenon skujae*, *Limnothrix planctonica* and *L.*
 245 *redekei* (*Limnothrix* taxa contributed together 40-75% of the total biomass in each sample), the
 246 dinoflagellates *Ceratium hirundinella* and *Peridinium* spp, the cryptophyte *Cryptomonas* spp., and
 247 the diatoms *Aulacoseira* sp., *Aulacoseira ambigua* and *Stephanodiscus astraea*. The high biomass
 248 contribution of the benthic diatom *Surirella robusta* in one sample indicated resuspension from the
 249 lake bottom sediments.

250

251 For Pyhäjärvi, the number of phytoplankton taxa with >5% biomass share during stratification was
 252 less than in Müggelsee, and was comprised of one cyanobacterium taxon (*Gomposphaeria*
 253 *aponina*), four diatom taxa (*Asterionella formosa*, *Fragilaria crotonensis*, *Tabellaria flocculosa* and
 254 *T. flocculosa* v. *asterionelloides*) and two dinoflagellate taxa (*Ceratium hirundinella* and
 255 *Gymnodinium* spp.). As for Vortsjärvi, the large diatom *Surirella robusta*, typically occurring in the
 256 sediment, co-dominated the phytoplankton biomass in two samples taken during stratification. The
 257 same taxa had often >5% share of the total phytoplankton biomass during the mixing/weak
 258 stratification together with the straight and curved *Anabaena* filaments, *Cryptomonas* spp.,
 259 *Plagioselmis lacustris*, unidentified centric diatoms, *Cyclotella meneghiniana*, *Melosira varians*,
 260 the chrysophytes *Mallomonas akrokomos*, *M. caudata* and *Uroglena* sp., and the prymnesiophyte
 261 *Chrysochromulina* sp.. During mixing events the cyanobacteria taxa *Anabaena* and *Planktothrix*
 262 increased ten-fold in biomass, although their biomasses were still rather low (0.07-0.1 mg l⁻¹). Also
 263 the total biomass of littoral/benthic algal taxa (e.g. the diatoms *Surirella* and *Entomoneis*) increased
 264 three-fold during mixing.

265

266 Diversity and abundance of zooplankton (total number of individuals, taxa number H' diversity and
 267 evenness) did not differ between the stratification and mixing episodes (Table 4).

268 Discussion

269 The thermal regime of our study lakes with frequent disruptions in stratification differs from that
 270 normally found in dimictic lakes where stable thermal stratification with little interannual variability
 271 in water temperature prevails from the onset of stratification in early summer to autumn partial
 272 degradation of stratification and the following complete turnover in autumn (Nöges et al. 2011). In
 273 our lakes, the average water temperature difference during stratification between the surface and
 274 bottom water layers of Müggelsee and Säkylän Pyhäjärvi were approximately only 3 °C, because of
 275 already warm hypolimnetic waters. This resulted in a relatively low water column stability making
 276 lakes prone to wind induced mixing and internal seiche effects (e.g. Wilhelm & Adrian 2008).
 277 [Comment to somewhere, that stratification in the years considered here never (?) surpassed critical
 278 lengths of >3 weeks to promote cyanobacteria dominance in Müggelsee.....]

279

280

281 The most discernible difference between the strength of stability and chemical parameters were, as
 282 expected, lower dissolved O₂ concentrations in the hypolimnion and the increased concentrations of
 283 inorganic P and N, and Fe in the hypolimnion (e.g. Niemistö et al. 2009). In Müggelsee the
 284 dissolved O₂ concentrations in the hypolimnion were clearly higher during stratification than in

285 Säkylän Pyhäjärvi, suggesting that Säkylän Pyhäjärvi may be more prone than Müggelsee to
 286 depletion of O₂ that promotes internal nutrient pulses (Wilhelm and Adrian 2008). Accumulation of
 287 inorganic nutrients in the hypolimnion during stratified periods and their transport to surface waters
 288 by mixing after the breakdown of stratification increased phytoplankton biomass in the epilimnion
 289 during summer, a phenomenon reported already earlier for Müggelsee (Wilhelm and Adrian 2008,
 290 Wagner and Adrian 2009). This suggests that the alternation of stratification and mixing episodes
 291 during summer in shallow eutrophic and polymictic lakes supplies recycled nutrients to the
 292 epilimnion and thus diminishes phosphorus limiting conditions for phytoplankton growth (see
 293 Padisák et al. 2010).

294
 295 Cyanobacteria and the diatoms, in particular the centric taxa belonging to the order Eupodiscales
 296 increased during periods of mixing. In addition to increased nutrients the increase in diatoms results
 297 from the increased turbulence as the diatoms are good competitors during such conditions (Willén
 298 1991). However, it is evident that part of the increase in the biomass of cyanobacteria and diatoms
 299 resulted from resuspension of sedimented algal cells back to the water column (Nõges et al. 2010).
 300 This was supported by the increased turbulence (Table 3) during mixing periods and also by the
 301 higher total biomass of benthic/littoral diatom taxa with heavy frustules in the pelagial samples; the
 302 taxa that would otherwise sediment rapidly to the bottom.

303
 304 Intermittent disturbances, like the mixing events, have been suggested to be responsible for high
 305 species diversity (Connell 1978, Polishchuk 1999), which is also experimentally shown for lakes
 306 (Gaedeke & Sommer 1986, Flöder & Sommer 1999). Flöder and Sommer (1999) found a clear
 307 maximum in phytoplankton diversity at the intermediate disturbance interval of six days under
 308 controlled field experiments, and a decrease in diversity with high frequency of disturbance. In our
 309 lakes, taxa richness or Shannon diversity [use the same name always] did not differ during the
 310 stratification and mixing episodes, possibly because our plankton composition data was, with the
 311 exception of Müggelsee, rather limited for comparison. It is possible that diel variations in stability
 312 of polymictic lakes (see Wilhelm & Adrian, 2008) in concert with frequent seasonal mixing
 313 maintained the level of turbulence that was for most of the summer intense and frequent enough to
 314 control phytoplankton competition (Polishchuk 1999). In contrast, during longer periods of mixing,
 315 evenness of phytoplankton decreased, as a result of higher biomass proportions of a rather few
 316 cyanobacterial and diatom taxa that benefited from turbulence. Earlier Wilhelm and Adrian (2008)
 317 and Wagner and Adrian (2011) have pointed out that albeit the diversity as such does not
 318 necessarily change due to changes in thermal regime, there can be changes in important functional

319 traits. For instance, increased dominance by cyanobacteria may affect nutrient recycling and
 320 nutrient stoichiometry via N-fixation. Filamentous cyanobacteria are also poor food for zooplankton
 321 which may be reflected to upper food web. Our zooplankton data was too scarce to notice
 322 differences in zooplankton composition or diversity between the mixed and stratified periods. In
 323 Müggelsee a rise a rise in the relative portion of thermophilic copepod species was observed during
 324 events of stratification exceeding a length of 4 weeks (Wagner and Adrian 2011). Zooplankton
 325 species with high thermal tolerances (i.e. *Thermocyclops oithonoides*, *Thermocyclops crassus*) and
 326 /or those that grow quickly at high temperatures (i.e. rotifers) became more common.

327
 328 The results from the three shallow, eutrophic and frequently mixing European lakes highlighted the
 329 importance of stratification and mixing events in shaping nutrient and oxygen concentrations in the
 330 water column. The results help to understand the impacts of climate-induced changes in thermal
 331 regime of lakes (e.g. Snucins & Gunn 2000, Arvola et al. 2010, Jones et al. 2010). Despite variation
 332 in stratification did not clearly affect the plankton diversity, the phytoplankton composition changed
 333 at group level which may affect ecosystem functionality (Wagner & Adrian 2011). Stratification
 334 event length and stability need to surpass critical thresholds in order to affect relative species
 335 composition, functionality, etc.....Wagner and Adrian, 2009, 2011.... The results are best
 336 applicable to shallow polymictic lakes, where the temperature difference between epi- and
 337 hypolimnion is low (during stratified periods), but appreciating that each lake behaves differently to
 338 climatic forcing (Blenckner et al. 2010) depending on morphometry, and the plankton community is
 339 under continuous interrelation with chemical and biological components of the ecosystem (Padisák
 340 et al. 2011). Like in polymictic lakes, the changes in mixing regime of dimictic lakes may result
 341 from temperature effects and/or precipitation- or reacidification related changes in dissolved
 342 organic carbon (water colour) load from the catchment that affects heat content (Houser 2006,
 343 Monteith et al. 2007, Hongve et al. 2004). For instance, an artificial deepening of the thermocline in
 344 a small humic lake in Southern Finland decreased N concentrations in the epilimnion (Forsius et al.
 345 2010, Verta et al. 2010).

346 347 **Acknowledgements**

348
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484

485 **Figure captions**

486

487

488 **Fig 1** Temporal variability of Schmidt stability ($J m^{-2}$) in June-August 2008-2011 in the studied
 489 lakes: a) Pyhäjärvi (FI) and Müggelsee (DE) and b) Vörtsjärv (EST). Grey vertical lines separate
 490 different years. Horizontal dotted line shows the Schmidt stability of $3.5 J m^{-2}$ used as criteria to
 491 separate stratified and mixed periods.

492

493 **Fig 2** Periods with stratification (Schmidt stability $>3.5 J m^{-2}$) (black lines) by week in June-August
 494 2008-2011 in the studied lakes: Säkylän Pyhäjärvi (FI), Vörtsjärv (EST) and Müggelsee (DE). The
 495 length of the line indicates the duration of the respective stratification episode. Grey areas indicate
 496 the periods with the stability data, white areas indicate the absence of stability data.

497

498 **Fig 3** Water column stability ($J m^{-2}$) and the biomass of cyanobacteria ($mg l^{-1}$) in May-September
 499 2009 in L. Säkylän Pyhäjärvi.

500

501

Table 1. Characteristics of the study lakes.

Lake	Country	Lake characterisation	Lake area (km ²)	Lat	Lon	Volume (km ³)	Mean depth (m)	Max depth (m)	Retention (year)
Müggelsee	Germany	eutrophic, polymictic	7.3	52°26'N	13°39'E	0.036	4.9	8.0	0.12
Võrtsjärv	Estonia	eutrophic, polymictic, fluctuating water level	270	58°17'N	26°02'E	0.75	2.8	6.0	1
Pyhäjärvi	Finland	eutrophic, polymictic	155	61°00'N	22°18'E	0.85	5.5	26.0	>4

Table 2. Difference in water temperature (WT °C) between the surface and bottom layers in the June-August samples as defined for the stratified periods (Schmidt stability $>3.5 \text{ J m}^{-2}$) and for the weakly stratified/mixing periods (Schmidt stability $\leq 3.5 \text{ J m}^{-2}$).

Lake	Stratified (stability $>3.5 \text{ J m}^{-2}$) difference in WT (°C)				Mixing/weakly stratified (stability $\leq 3.5 \text{ J m}^{-2}$) difference in WT (°C)			
	mean	min	max	n	mean	min	max	n
Müggelsee	3.2	0.7	9.2	37	0.2	0	2.5	98
Vörtsjärv	5.8	3.7	7.8	6	0.1	0	1.3	189
Pyhäjärvi	3.8	1.3	7.5	36	0.6	0.2	1.6	69

Table 3. Summary statistics (mean ± SD) of physico-chemical variables during periods of stratification (Schmidt stability >3.5 J m⁻²) and mixing/weak stratification (Schmidt stability ≤3.5 J m⁻²) in June-August in the epilimnion (epi) and hypolimnion (hypo) of studied lakes. n = number of observations. Significant differences between the stratified and mixing periods shown as bold (p<0.001) or underlined (p<0.05).

Variable	Pyhäjärvi (FI)						Vörtsjärv (EST)						Müggelsee (GER)					
	>3.5 Jm ⁻²		≤3.5 Jm ⁻²		Mann-Whitney p	>3.5 Jm ⁻²		≤3.5 Jm ⁻²		Mann-Whitney p	>3.5 Jm ⁻²		≤3.5 Jm ⁻²		Mann-Whitney p			
	mean ± SD	n	mean ± SD	n		mean ± SD	n	mean ± SD	n		mean ± SD	n	mean ± SD	n				
Stability (J m ⁻²)	12.6±9.3	38	1.2±0.8	70	0.000	5.8±1.7	6	0.1±0.6	251	0.000	16.9±15.2	26	0.7±1.2	26	0.000			
WT (°C) epi	18.6±1.8	38	16.7±2.1	70	0.000	24.8±1.6	6	19.6±3.5	141	0.001	21.3±1.6	26	19.7±1.4	25	0.001			
WT (°C) hypo (2.5m)	15.6±2.2	38	16.4±2.1	70	0.154	22.6±1.9	6	19.7±3.6	142	<u>0.043</u>	19.5±1.1	24	18.6±1.4	22	<u>0.029</u>			
Dissolved O ₂ (mg l ⁻¹) epi	9.7±0.4	38	9.8±0.3	70	0.160	10.1±1.3	6	9.7±1.3	233	0.314	19.4±5.2	24	17.1±5.2	26	<u>0.016</u>			
Dissolved O ₂ (mg l ⁻¹) hypo	5.5±2.3	38	8.4±1.5	70	0.000	n.a.		n.a.			14.2±7.3	22	16.2±6.2	24	0.085			
Turbidity FNU epi	1.8±0.6	37	2.8±0.8	62	0.000	n.a.		n.a.			n.a.		n.a.					
PO ₄ -P (µg l ⁻¹) epi	1.8±1.6	5	2.8±1.6	7	0.268	n.a.		n.a.			77.0±84.1	26	134.7±105.8	27	0.003			
PO ₄ -P (µg l ⁻¹) hypo	16.2±8.1	5	7.4±5.0	7	<u>0.030</u>	n.a.		n.a.			179.0±154.2	26	151.6±150.8	5	0.696			
Total P (µg l ⁻¹) epi	19±3	5	20±4	7	0.755	n.a.		n.a.			154±98	26	221±115	27	<u>0.010</u>			
Total P (µg l ⁻¹) hypo	37±10	5	30±8	7	0.343	n.a.		n.a.			272±187	26	228±150	5	0.735			
NO ₂ +NO ₃ -N (µg l ⁻¹) epi	11±11	5	10±11	7	0.639	n.a.		n.a.			42.7±60.3	26	27.8±36.7	27	0.247			
NO ₂ +NO ₃ -N (µg l ⁻¹) hypo	15.5±13.4	5	9.3±9.9	7	0.106	n.a.		n.a.			48.4±61.8	25	22.0±26.4	5	0.355			
NH ₄ -N (µg l ⁻¹) epi	6.5±9.3	5	6.8±6.2	7	0.755	n.a.		n.a.			83.1±79.3	26	123.0±122.1	27	0.214			
NH ₄ -N (µg l ⁻¹) hypo	180.4±117.0	5	37.1±73.6	7	<u>0.018</u>	n.a.		n.a.			261.5±208.1	24	195.0-234.8	5	0.352			
Total N (µg l ⁻¹) epi	402±20	5	432±27	7	0.106	n.a.		n.a.			1009±173	26	1073±183	27	0.301			
Total N (µg l ⁻¹) hypo	593±119	5	475±73	7	<u>0.030</u>	n.a.		n.a.			1143±225	26	1140±230	5	0.979			
SRSi (mg l ⁻¹) epi	n.a.		n.a.			n.a.		n.a.			3.5±2.4	26	4.5±2.3	27	0.113			
SRSi (mg l ⁻¹) hypo	n.a.		n.a.			n.a.		n.a.			4.8±2.6	26	5.0±2.3	5	0.548			
Fe (µg l ⁻¹) epi	77±36	5	101±40	7	0.343	n.a.		n.a.			n.a.		n.a.					
Fe (µg l ⁻¹) hypo	271±58	5	208±80	7	0.149	n.a.		n.a.			n.a.		n.a.					

Table 4. Summary statistics (mean ± SD) of plankton abundance, biomass, taxa numbers, Shannon diversity index and Evenness during the periods of stratification (Schmidt stability >3.5 J m⁻²) and mixing/weak stratification (Schmidt stability ≤3.5 J m⁻²) in June-August in the epilimnion (epi) and hypolimnion (hypo) of studied lakes. n = the number of observations. Significant differences between the stratified and mixing periods shown as bold (p<0.001) or underlined (p<0.05).

Variable	Pyhäjärvi				Mann-Whitney p	Vörtjärvi				Mann-Whitney p	Müggelsee				Mann-Whitney p
	>3.5 Jm ²		≤3.5 Jm ²			>3.5 Jm ²		≤3.5 Jm ²			>3.5 Jm ²		≤3.5 Jm ²		
	mean ± SD	n	mean ± SD	n		mean ± SD	n	mean ± SD	n		mean ± SD	n	mean ± SD	n	
Phytoplankton															
Chlorophyll <i>a</i> (µg l ⁻¹)	3.8 ± 2.0	37	8.2 ± 3.7	68	0.000	35.3 ± 0.51	4	45.5 ± 9.12	169	<u>0.012</u>	39.4 (11.1-81.4)	26	37.3 (9.6-100.5)	27	0.364
Total biomass (mg l ⁻¹)	0.62 ± 0.17	3	2.54 ± 1.82	6	<u>0.024</u>	n.a.		22.04 ± 4.22	9		6.65 (1.07-18.13)	26	6.14 (0.53-15.97)	27	0.887
Cyanobacteria (mg l ⁻¹)	0.10 ± 0.07	37	0.32 ± 0.25	68	0.000	13.0 ± 0.99	4	11.8 ± 2.81	94	0.258	1.76 (0.01-8.19)	26	1.51 (0.04-11.01)	27	0.444
Species richness (no of taxa)	59 ± 16	3	62 ± 13	6	1.000	n.a.		34 (26-48)	9		13 (7-22)	26	13 (8-21)	27	0.796
No of taxa with >5% tot-biom	4.2 ± 1.6	3	4.3 ± 1.6	6	0.714	n.a.		3 (2-4)	9		4 (1-7)	26	4 (1-7)	27	0.271
Diatom biomass (mg l ⁻¹)	0.26 ± 0.08	3	1.92 ± 2.31	6	0.229	n.a.		5.62 (2.41-9.43)	9		3.17 (0.001-16.37)	26	3.86 (0.02-11.617)	27	0.434
Eupodiscales (mg l ⁻¹)	0.01 ± 0.003	3	0.39 ± 0.45	6	<u>0.024</u>	n.a.		3.83 (1.04-7.32)	9		2.95 (0-16.36)	26	3.76 (0.01-11.50)	27	0.262
Pennales (mg l ⁻¹)	0.26 ± 0.08	3	1.34 ± 1.92	6	0.167	n.a.		1.45 (0.40-3.31)	9		0.22 (0-2.20)	26	0.10 (0-0.47)	27	0.855
Chlorophyceae (mg l ⁻¹)	0.03 ± 0.008	3	0.07 ± 0.02	6	0.057	n.a.		0.37 (0.11-0.81)	9		0.27 (0.01-0.86)	26	0.08 (0.01-0.32)	27	0.003
Dinophyceae (mg l ⁻¹)	0.05 ± 0.04	3	0.04 ± 0.03	6	0.629	n.a.		2.31 (0.11-11.55)	9		0.28 (0-1.41)	26	0.26 (0-1.15)	27	0.566
Diversity (Shannon by biomass)	1.26 ± 0.20	3	1.13 ± 0.27	6	0.629	n.a.		0.77 (0.53-0.98)	9		0.63 (0.05-1.05)	26	0.63 (0.26-0.88)	27	0.119
Evenness	0.71 ± 0.07	3	0.64 ± 0.12	6	0.857	n.a.		0.50 (0.34-0.58)	9		0.53 (0.06-0.81)	26	0.57 (0.27-0.81)	27	0.063
Zooplankton															
Total number (10 ⁵ ind. m ⁻²)	6.51 ± 1.61	3	8.29 ± 2.02	5	0.786	n.a.		72.9 (32.7-140.3)	9		26.2 (54.2-82.8)	26	25.6 (12.9-53.9)	27	0.957
Richness (no of taxa)	n.a.		n.a.			n.a.		15.3 (12-21)	9		36 (29-48)	20	35 (25-47)	20	0.578
Diversity (Shannon by abundance)	0.76 ± 0.04	3	0.81 ± 0.04	5	1.000	n.a.		0.65 (0.44-0.84)	9		1.04 (0.82-1.31)	20	1.03 (0.83-1.35)	20	0.929
Evenness	0.74 ± 0.08	3	0.77 ± 0.03	5	1.000	n.a.		0.56 (0.37-0.78)	9		0.66 (0.53-0.78)	20	0.66 (0.51-0.83)	20	1.000
Cladocera number (10 ⁵ ind. m ⁻²)	1.8 ± 1.3	3	3.3 ± 1.8	5	0.393	n.a.		4.5 (0.1-31.0)	9		2.1 (0.02-13.5)	26	1.7 (0.01-13.3)	27	0.204
Cyclopoida number (10 ⁵ ind. m ⁻²)	4.7 ± 1.6	3	5.0 ± 1.1	5	1.000	n.a.		7.3 (3.0-11.4)	9		2.0 (0.4-4.7)	26	2.3 (0.3-5.6)	27	0.797
Rotifera number (10 ⁵ ind. m ⁻²)	n.a.		n.a.			n.a.		62.4 (5.2-132.0)	9		20.0 (3.3-76.8)	26	19.1 (3.2-49.5)	27	0.745

Fig 1.

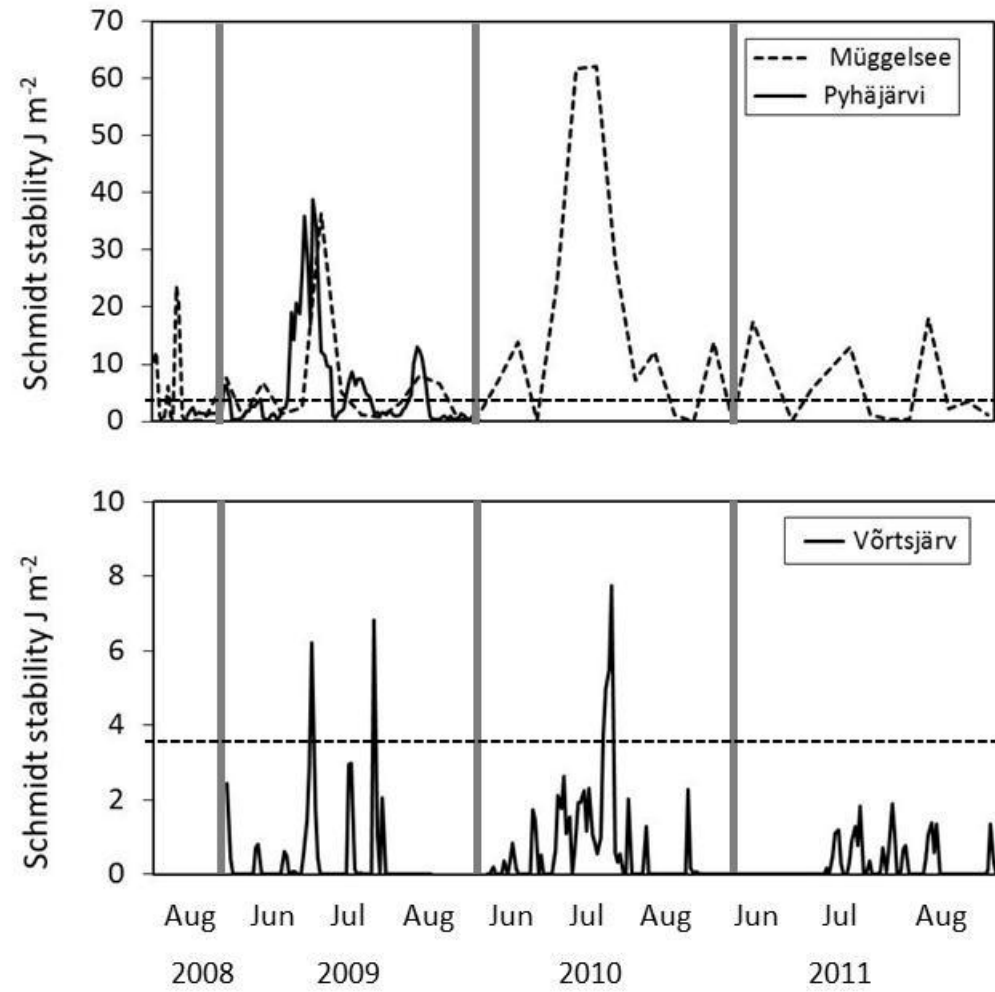


Fig. 2

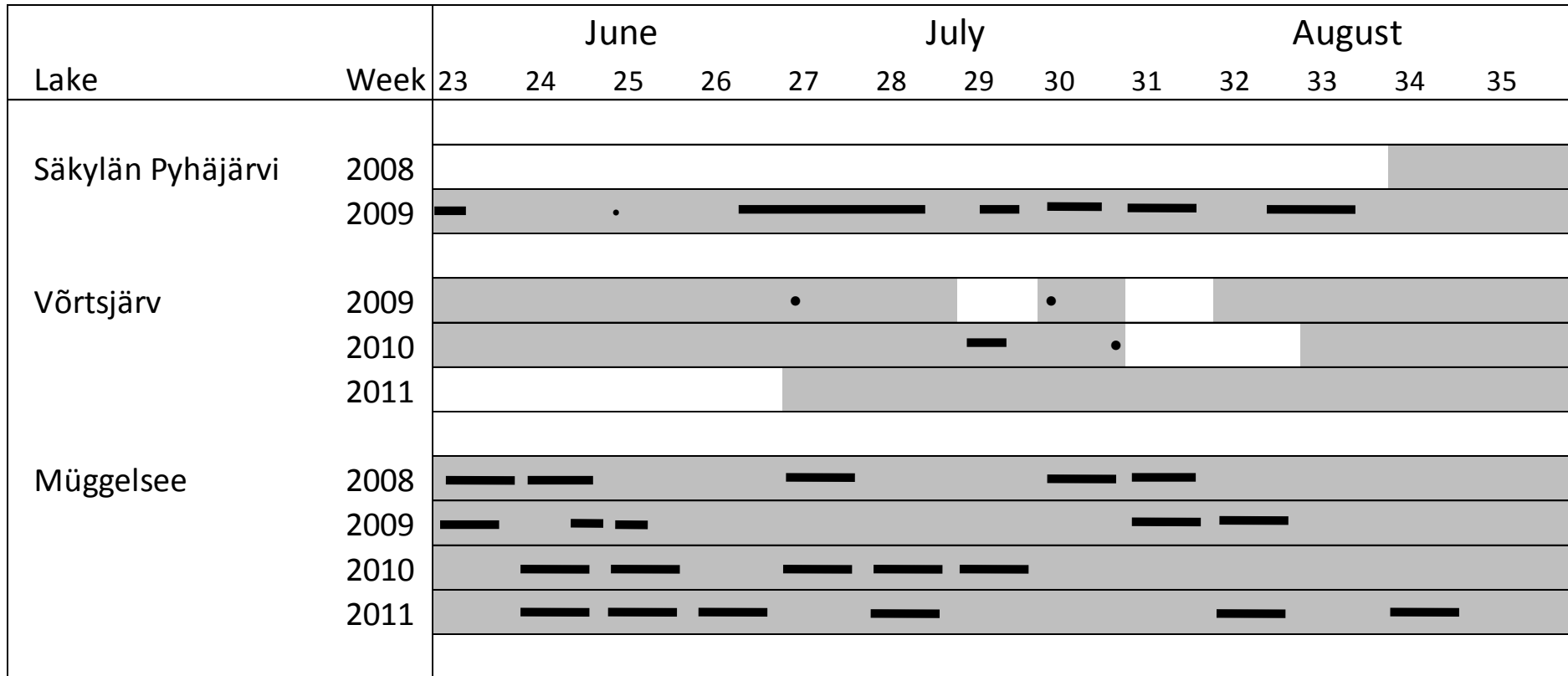


Fig 3

