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1 The role of internal feedbacks in shifting deep lake mixing regimes under a warming climate

2
3 *Running title: Feedbacks and mixing regimes in deep lakes*

4
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21 **Abstract**

22 Climate warming is causing changes in the physics of deep lakes, such as longer summer
23 stratification, increased water column stability, reduced ice cover, and a shallower depth of
24 winter overturns. An ultimate consequence of warming would be a transition to a different
25 mixing regime. Here we investigate the role of physical, chemical, and biological feedback

26 mechanisms that unfold during a shift in mixing regime, and whether these feedbacks could
27 prompt and stabilise the new regime. Although climate, interannual temperature variation, and
28 morphometry are the main determinants of a mixing regime, when climate change causes
29 shifts in mixing regime, internal feedback mechanisms may gain in importance and modify
30 lake ecosystem functioning.

31 We review the role of these feedbacks in shifts from 1) polymictic to seasonally stratified,
32 2) dimictic to monomictic, and 3) holomictic to oligomictic or meromictic. 1) Polymictic
33 lakes of intermediate depth could experience seasonal stratification if a stratification event
34 triggers phytoplankton blooms or dissolved organic matter release, reducing transparency and
35 therefore further heating the surface layers. However, this feedback is only likely to have
36 influence in small and clear lakes, might be easily disturbed by weather conditions, and the
37 resulting stratified state does not remain stable in the long term, as stratification is lost in
38 winter. 2) The ice-albedo feedback might cause an accelerated shift from ice-covered to ice-
39 free water in sufficiently deep lakes, where temperature memory is carried over from one
40 winter to the next. Nevertheless, there is ongoing debate whether this process can persist
41 during natural weather variations and overcome the self-stabilising mechanisms present in the
42 system. 3) A shift from a holomictic to a meromictic regime can occur if anoxia is triggered
43 by incomplete mixing and an increase in deep-water density - through the accumulation of
44 solutes - exceeds a density decrease by hypolimnetic warming. A shift to meromixis would
45 strongly alter the ecology of a lake and might be difficult to reverse. If solutes do not
46 accumulate in the hypolimnion, an oligomictic regime is formed, in which years with
47 complete and incomplete mixing alternate.

48

49

50 **Introduction**

51 Temperatures in lakes all over the world have been rising over the past century as a
52 consequence of global warming (O'Reilly et al., 2015). This warming has resulted in an
53 overall increase in thermal stability, with longer periods of summer stratification and steeper
54 thermoclines, restricting exchange of substances between the epi- and hypolimnion (Kraemer
55 et al., 2015; Shimoda et al., 2011). Climatic trends driving the thermal stability in deep lakes
56 have also had profound impacts on lake chemistry and biology. For instance, reduction of
57 deep mixing can result in the depletion of oxygen (anoxia) in the hypolimnion (Schwefel et
58 al., 2016). A longer duration of stratification and reduction of deep mixing can increase the
59 heterogeneity of vertical nutrient profiles, with nutrient-rich deep waters and nutrient-poor
60 surface waters (Schwefel et al., 2019; Winder & Sommer, 2012). In turn, this altered vertical
61 nutrient distribution affects lake biota such as phytoplankton and fish (O'Reilly et al., 2003;
62 Winder & Sommer, 2012). Moreover, both observational studies of lake thermal structure and
63 numerical climate simulations have pointed towards climate-induced shifts in mixing regime
64 (Box 1), implying structural changes in lake ecosystems (Ficker et al., 2017; Peeters et al.,
65 2002; Shatwell et al., 2019; Woolway & Merchant, 2019).

66

67 In the present review paper we look at the physical, chemical, and biological consequences of
68 climate warming and density stratification in deep lakes – defined here as lakes that stratify
69 during at least one season. We then identify internal feedbacks that can reinforce (positive
70 feedbacks) or slow down (negative feedbacks) shifts between mixing regimes. The scope of
71 this paper only includes regime shifts where such feedback loops were identified in existing
72 literature, or where they could be constructed using individual processes, and considers
73 regime shifts during a period of increasing temperatures. The potential importance of
74 feedbacks is well illustrated by the alternative macrophyte- (clear-water) and algae-dominated
75 (turbid) states in shallow lakes. Regime shifts between these two states involve feedback

76 loops between turbidity, nutrients, and trophic interactions that retain either state in the face of
77 external perturbations (Scheffer, 1998; Scheffer et al., 2001).

78

79 In deep, stratified lakes the vertical distribution of oxygen, nutrients, and phytoplankton are
80 strongly influenced by density stratification, which hints at the potential of mixing regimes to
81 act as important drivers of ecosystem state. Mixing regimes are primarily driven by physical
82 processes, and therefore under direct influence of climate change (Livingstone, 2008) (for
83 definitions of mixing regimes, see Box 1). Mixing regimes in deep lakes differ from one
84 another in several physical, chemical, and biological aspects (e.g. Adrian et al., 2009; Boehrer
85 & Schultze, 2008; North et al., 2014).

86 According to the classical view on mixing regimes (Hutchinson & Löffler, 1956; Lewis Jr,
87 1983), local climate and morphometry are the main factors determining the mixing regime of
88 a lake. However, factors other than depth and climate, such as transparency (Brothers et al.,
89 2014) and solute content (Boehrer & Schultze, 2008), can also influence lake mixing.

90 Conversely, mixing regimes might influence these factors. Thus, lake-internal feedbacks
91 could stabilise and even determine the mixing regime, especially in situations where
92 morphometry and climate can support multiple mixing regimes. It is in these situations that
93 mixing regime shifts are to be expected in response to ongoing climate change. If self-
94 sustaining feedback mechanisms hold the new regime in place, shifts in mixing regime may
95 be more permanent and resilient than expected.

96

97 Quantitative observations and numerical simulations specifically focusing on shifts in mixing
98 regime by factors other than temperature are scarce, as long-term observations and detailed
99 studies are needed to observe such shifts and identify the drivers. However, individual
100 processes that could lead to feedback loops stabilising mixing regimes, are well described. In

101 what follows, we review the literature on the physical trends related to increased duration and
102 strength of density stratification, and the chemical and biological consequences thereof
103 (Figure 1). Following this literature review, we derive processes at play during a transition in
104 mixing regime are derived and discuss their interaction in typical lake regime shifts. The
105 observed feedbacks are brought together, visualised, and placed into the perspective of shifts
106 in mixing regime under increasing temperatures. We also discuss the limitations of the
107 relevance of each feedback and specify for what types of lakes these feedbacks may be
108 considered. In this way, we believe our review provides new and pertinent information on
109 how climate warming may affect lake ecosystems, extending beyond direct effects of
110 temperature alone.

111

Box 1: Types of lake mixing regimes

Categorising lakes on the basis of their mixing regime is a well-established practice (Forel, 1880; Hutchinson & Löffler, 1956). Lakes are classified according to the number of mixing events per year and the degree of mixing. Depending on climate zone, depth, salinity, and lake morphology, a lake mixes a certain number of times per year (0- amictic, 1- monomictic, 2-dimictic, 3 or more- polymictic), either completely – always from top to bottom (holomixis) –, only sometimes from top to bottom (oligomixis) or only partially (meromixis). Shallow lakes tend to be *polymictic*, i.e. they mix multiple times per year. Below what depth a lake is to be considered “shallow” has been the topic of discussion (see Padisák & Reynolds, 2003). In most cases, the occurrence of polymixis is used to define a lake as “shallow”. Depending on lake fetch, transparency, and wind speeds, polymixis tends to occur below mean depths of 3 to 20 m (Kirillin & Shatwell, 2016; Padisák & Reynolds, 2003). This shallowness makes the lake prone to mixing events, either wind-induced or caused by convective cooling, although stratification events lasting multiple

days or weeks are also possible (Mischke, 2003; Wilhelm & Adrian, 2008).

The presence of long-term density stratification is used by us to define what constitutes a deep lake. In deep lakes, seasonal temperature variation largely controls the mixing regime. Near the poles, lakes, for now, have permanent ice cover (*amictic lakes*) or only experience inverse stratification (i.e. cold above warmer water, as the maximum density of freshwater is achieved at 4 °C) and these *cold monomictic* lakes only mix in summer. Moving to lower latitudes, winter temperatures are still cold enough for inverse stratification and ice formation, but air temperatures in summer are high enough to allow formation of a warm epilimnion; these are *dimictic* lakes, that mix before and after a winter period with inverse stratification. Where winters are not cold enough for ice formation, stratification only occurs in summer and deep lakes only mix in winter: these are *warm monomictic* lakes (Lewis Jr, 1983). The distribution of deep lake mixing regimes is largely climate-controlled. The absence of strong seasonal temperature variation in tropical regions causes a different yearly pattern near the equator, with a more dynamic development of the epilimnion. However, mixing seasons often still exist as a result of seasonal patterns in radiation, rainfall, or wind, and tropical deep lakes are classified as warm monomictic, following Lewis Jr (1996). In the main text the term “monomictic” refers to warm monomictic lakes.

Winter mixing does not necessarily reach the deepest location of the lake. Complete mixing is called *holomixis* and incomplete mixing is termed *meromixis*. In permanent or “true” meromictic lakes, stratification is caused by an increased concentration of solutes that raises the density of the deep water, for example by sea water or saline groundwater influx (Gulati et al., 2017; Hutchinson, 1957). The two chemically-different layers do not mix for multiple

years. However, in many temperate and tropical deep lakes, mixing depths vary year-to-year and complete winter mixing occurs at varying frequencies, ranging from on average once every year to once every five decades. These lakes are not holomictic, but no permanent chemical stratification is formed either. In this paper we define these lakes as *oligomictic* (following Lewis Jr, 1973). The term *meromictic* is reserved for lakes with chemically different layers and stable density stratification due to the effect of solutes (following Gulati et al., 2017).

We therefore define the mixing regime of a lake both in terms of the frequency of mixing (poly-, di-, monomictic) and the extent of mixing (holo-, oligo-, meromictic). For a more complete description of mixing regimes and potential further subdivisions, we refer the reader to Boehrer and Schultze (2008).

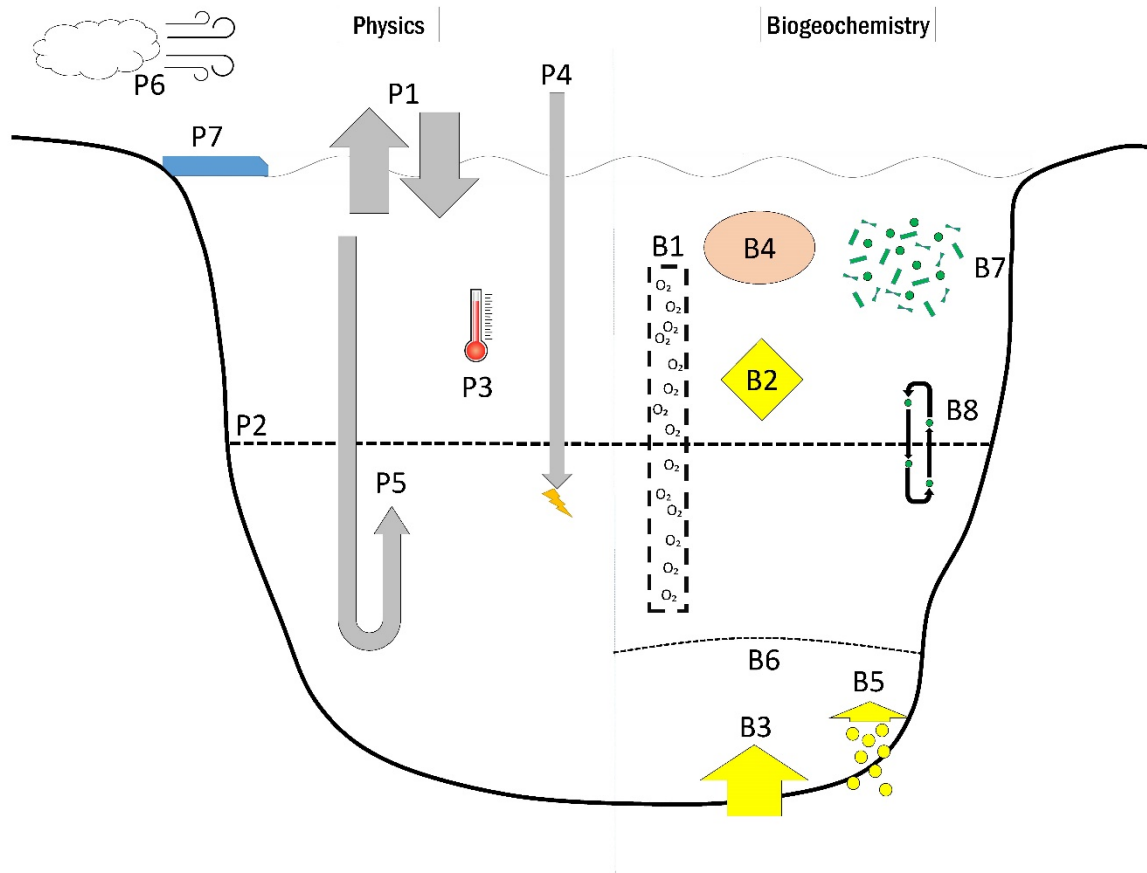
112

113

114 **Physical, chemical, and biological consequences of enhanced stratification**

115 *Figure 1: Overview of the physical, chemical and biological components and processes in*
116 *deep lakes considered in the text. Energy fluxes at the air-water interface (P1) represent the*
117 *interaction between climate and the lake. Thermal stratification (P2) is important for*
118 *transport between water layers, and is formed primarily by higher water temperatures (P3) in*
119 *the surface layers compared to bottom layers. Light penetration (P4) causes heating of*
120 *surface layers and is essential for phytoplankton growth. Deep-water mixing (P5) can occur*
121 *as a result of strong convective cooling and marks the end of the stratified season. Wind*
122 *stress (P6) also promotes mixing and deepening of the mixed layer. Ice cover (P7) affects*
123 *surface heat fluxes and reduces effects of wind on the lake interior. Oxygen concentration*
124 *(B1) is linked to many chemical and biological processes in the water column. Nutrient*
125 *concentrations (B2) in the epilimnion are essential for the growth of phytoplankton. Nutrients*

126 and other type of solutes can be released from the sediment (B3). Coloured dissolved organic
 127 matter (CDOM, B4) reduces light penetration in the water column. Greenhouse gases can be
 128 emitted from the sediment (B5). In case the deep-water layers of a lake are heavier than the
 129 overlying water due to solute content, meromixis is formed (B6). Phytoplankton biomass (B7)
 130 grows on nutrients and light in the photic zone of the lake. Some phytoplankton species have
 131 variable buoyancy (B8) that enables uptake of nutrients from below the thermocline.



132

133 Water temperatures and stratification

134 (Figure 1: P1, P2, P3) The increase in global surface air temperature (IPCC, 2014) has an
 135 impact on lake temperature and water column stratification. Global surveys of surface water
 136 temperatures report an increase in epilimnetic temperatures with rates roughly between 0.2
 137 and 1 °C per decade (Kraemer et al., 2015; O'Reilly et al., 2015; Shimoda et al., 2011). The
 138 temperature difference between epi- and hypolimnion often increases, causing longer and
 139 stronger thermal stratification in summer (Fang & Stefan, 1999; Foley et al., 2012; Kraemer et

140 al., 2015). Even when temperature differences remain the same, the density difference
141 becomes greater with warming, as the water density-temperature relation is steeper at higher
142 temperatures (Wetzel, 2001). As the density difference between epi- and hypolimnion
143 increases, mixing of the two layers is reduced, which further heats the surface layer and
144 increases density differences, as less heat is transported downwards. The stability of the water
145 column is often expressed as the Schmidt stability (i.e. the potential energy stored in
146 stratification per unit area) (Idso, 1973; Schmidt, 1928). Between 1970 and 2010, average
147 Schmidt stability in lakes worldwide has increased by up to 25% (Kraemer et al., 2015).

148

149 (Figure 1: P2) A larger density difference between the epilimnion and hypolimnion increases
150 the local stability of the water column. An increase in stability reduces the vertical turbulent
151 diffusivity K_z , which indicates the rate of vertical mixing (Ravens et al., 2000; Wüest et al.,
152 2000). Hence, a stronger stratification implies that dissolved substances less easily traverse
153 the thermocline, promoting separation between surface and bottom waters.

154

155 Oxygen dynamics in deep lakes

156 (Figure 1: P2, P4, P5, B1) Oxygen sources (reaeration and photosynthesis) are mainly
157 restricted to the epi- and metalimnion (Giling et al., 2017b; Obrador et al., 2014; Wetzel,
158 2001), and in most lakes oxygen is constantly being depleted in the hypolimnion. Generally,
159 the deeper layers receive oxygen from mixing with surface layers during the turnover periods,
160 although river intrusion can also notably affect hypolimnetic oxygen conditions (Fink et al.,
161 2016).. Deep convective mixing is often the major source of oxygen replenishment in the
162 deep-water layers (Straile et al., 2003), and it can quickly alleviate anoxic conditions
163 (Lehmann et al., 2015; Sahoo et al., 2013). The extent of the oxygen-depleting processes in
164 the water column and the sediment, the volume of the hypolimnion, and the sediment area to

165 hypolimnion volume ratio define the rate at which oxygen concentrations drop (Schwefel et
166 al., 2018). Hypolimnia of highly productive systems have a higher oxygen depletion rate
167 (Müller et al., 2012; Rippey & McSorley, 2009). Deeper lakes contain more oxygen due to a
168 thicker hypolimnion, and oxygen depletion rates tend to decrease with depth, so deeper lakes
169 are less prone to become anoxic in one summer (Müller et al., 2012; Schwefel et al., 2018).
170 However, they are less likely to experience complete vertical mixing, and climate warming
171 further decreases this likelihood. In the case of incomplete mixing, the oxygen is only
172 partially replenished and the hypolimnion will experience lower oxygen levels the following
173 year. Therefore, a shift from holomictic to oligomictic behaviour implies a greater risk of
174 anoxic conditions, for productive lakes in particular.

175

176 (Figure 1: P3, P5, B1) Numerous observations of hypolimnetic anoxia attributed to
177 shifts in the extent of mixing exist in both temperate (e.g. Foley et al., 2012; Ito & Momii,
178 2015) and tropical regions (e.g. Fukushima et al., 2017; O'Reilly et al., 2003), and climate
179 change is expected to amplify this trend (Fang & Stefan, 2009; Peeters et al., 2002; Sahoo et
180 al., 2013). While eutrophication is often seen as the main cause of anoxia, changes in deep-
181 water mixing can be at least as important in deep lakes (Schwefel et al., 2016). Aside from the
182 increase in stratification, climate change can affect hypolimnetic oxygen through increased
183 temperatures as well, as mineralisation and metabolic rates are higher at higher temperatures,
184 in the order of a 3-6% increase per °C (Fang & Stefan, 2009; Gudas et al., 2010). In this
185 way, hypolimnetic warming could increase the intensity of oxygen depletion in the
186 hypolimnion and sediments (Straile et al., 2003).

187

188 Influence of anoxia on nutrient distribution and other substances

189 (Figure 1: B1, B2, B3) Hypolimnetic anoxia can induce enhanced internal phosphorus
190 loading through reduction of the benthic redox potential, so that iron-bound phosphate is
191 released from the sediment (Søndergaard et al., 2003). While this release can be relevant on
192 short time scales, phosphorus is also released under oxic conditions, and on seasonal time
193 scales and longer, internal P budgets are mostly dependent on settling and mineralisation rates
194 and sediment characteristics (Hupfer & Lewandowski, 2008). During stratification, P tends to
195 accumulate in the hypolimnion as nutrients are not mixed into the photic zone while
196 mineralisation in the sediment and pelagic continues. When deep mixing occurs, oxygen
197 conditions near the surface can drop and large amounts of P can enter the photic zone,
198 potentially boosting productivity (Lehmann et al., 2015; Lepori et al., 2018a). Nitrogen can
199 also be released from the sediment under anoxic conditions in the form of ammonium
200 (Wetzel, 2001). In lakes where light reaches the sediment, benthic algae can take up this
201 release and expand their biomass, but this is often not the case in stratifying lakes.
202 Denitrification occurs in anoxic hypolimnia and, especially, sediments (Wetzel, 2001). It is a
203 major loss term of nitrogen in lakes. When anoxia of the hypolimnion is ended by a mixing
204 event, large losses of nitrogen to the atmosphere can occur through denitrification, as nitrate-
205 rich water is brought in contact with the anoxic sediment (De Brabandere et al., 2015;
206 Lehmann et al., 2015).

207

208 (Figure 1: P5, P6, B1, B2, B3) The stratification that is at the root of this build-up of
209 nutrients, however, also prevents nutrients from entering the epilimnion, as increased
210 stratification implies that dissolved substances are retained more in their respective layers.
211 Reduced entrainment of deeper water layers and less intense winter mixing could cause
212 decreased nutrient concentrations in the epilimnion, despite the higher nutrient concentrations
213 in the hypolimnion (Schwefel et al., 2019; Yankova et al., 2017). As nutrients accumulate in

214 the hypolimnion because of increased stratification with climate change, the amount of
215 nutrients released to the epilimnion when complete mixing does occur, goes up. Storms can
216 induce mixing events that bring deep-water nutrients to the surface (Crockford et al., 2015;
217 Soranno et al., 1997). [ENREF 75](#)

218

219 (Figure 1: B1, B3, B4, B5, B6) Apart from nitrogen and phosphorus, other substances
220 are affected by hypolimnetic shortages of oxygen as well. Iron-oxide-bound carbon can be
221 released as Coloured Dissolved Organic Matter (CDOM) under anoxia when iron is reduced
222 (Brothers et al., 2014; Hamilton-Taylor et al., 1996). In the deep layers of meromictic lakes,
223 the anoxic conditions enable the occurrence of reduction processes involving iron,
224 manganese, and sulphide, which are often essential for creating and maintaining meromixis
225 (Friedrich et al., 2014; Lehmann et al., 2015; Schultze et al., 2017). These elements can occur
226 in dissolved form under anoxic conditions and accumulate in deep-water layers of meromictic
227 lakes, where they increase deep-water density (Gulati et al., 2017; Imboden & Wüest, 1995).
228 Strong stratification and anoxia can also induce more methane emissions from lakes (Grasset
229 et al., 2018; Vachon et al., 2019). Like dissolved solutes, dissolved methane and dissolved
230 carbon dioxide can occur in high concentrations in deep, anoxic water layers, and affect
231 density, with methane reducing and carbon dioxide increase water density (Imboden &
232 Wüest, 1995; Schmid et al., 2002). The effect of dissolved gases on density can be especially
233 important in lakes where there is a high influx of gases from the sediment, for example as a
234 result of volcanic activity (Schmid et al., 2002).

235

236 Influence of mixing dynamics on lake phytoplankton

237 (Figure 1: B2, B7) A change in nutrients in the epilimnion will strongly control
238 phytoplankton development. As mentioned above, increased stratification might actually

239 reduce nutrient levels in the surface water of lakes. Longer stratification in such a case, means
240 a longer period of nutrient limitation for phytoplankton (Yang et al., 2016) and therefore more
241 advantage for species that efficiently use or store nutrients (Winder & Sommer, 2012), and
242 potentially for mixotrophic species, that have access to additional organic nutrient sources
243 (Jansson et al., 1996). However, the effects of increased stratification and warming of surface
244 waters differ between oligotrophic and eutrophic systems. In oligotrophic systems, a higher
245 metabolic rate driven by higher temperatures in combination with nutrient shortage can lead
246 to lower levels of biomass compared to colder temperatures, while in eutrophic systems the
247 higher temperature boosts growth and biomass (Jöhnk et al., 2008; Kraemer et al., 2017).

248

249 (Figure 1: P2, P4, B7, B8) Stratification also affects the phytoplankton's ability to remain
250 near the surface and in the euphotic zone. Formation of a thermocline reduces the depth over
251 which phytoplankton is mixed, effectively increasing their chance to remain in the photic
252 zone (Huisman et al., 1999). In contrast, stratification reduces turbulence and vertical mixing
253 deeper in the water column, and sinking becomes a major loss term for many dense
254 phytoplankton species (Diehl et al., 2002). A lower viscosity at higher temperatures (Hutter &
255 Jöhnk, 2004) increases sinking rates, , but also facilitates migration through buoyancy
256 regulation (Paerl & Huisman, 2009). Stronger density stratification and absence of turbulence
257 thus may give an advantage to motile phytoplankton species (Huisman et al., 2004; Winder &
258 Hunter, 2008).

259

260 (Figure 1: P5, B2, B7, B8) Higher nutrient concentrations in the hypolimnion do not
261 directly promote phytoplankton growth because of the lack of light at depth, with the
262 exception of phytoplankton species that produce a deep chlorophyll maximum in the
263 metalimnion (e.g. *Planktothrix rubescens*), or buoyancy regulators that are perceived to make

264 excursions into the hypolimnion (e.g. *Microcystis*) (Fee, 1976; Paerl & Huisman, 2009). The
265 strong vertical heterogeneity in nutrient levels induces the possibility that mixing events
266 causing entrainment of hypolimnetic water into the epilimnion can lead to spikes of
267 epilimnetic nutrient concentrations (Lehmann et al., 2015), stimulating phytoplankton blooms
268 (Giling et al., 2017a). These events can be caused by extreme weather events such as storms,
269 cold spells, or river floods (Jennings et al., 2012). With increased stratification in summer, the
270 amount of energy needed for these deep mixing events increases, but the nutrient pulse after
271 such an event tends to be stronger (Coats et al., 2006). Extreme weather events are projected
272 to become more frequent and intense in the future (Ummenhofer & Meehl, 2017) and will
273 interact with climatic trends, making the impact of extreme events on phytoplankton blooms
274 an important topic for further study.

275

276 **Shifts in mixing regime**

277 In this section we identify which processes could form positive or negative feedbacks that
278 could lead to a shift in mixing regime. As these shifts are likely to occur in the future
279 (Woolway & Merchant, 2019), it is important to assess which changes to expect and if they
280 are able to self-amplify under a given condition. The shifts in mixing regime that are treated
281 here are 1) from a polymictic to a seasonally stratified regime, 2) from a dimictic to a
282 monomictic regime, where ice cover and inverse stratification in winter are disappearing, and
283 3) from a holomictic to an oligomictic or a meromictic regime. Here we investigate if and
284 under what conditions feedback mechanisms can reinforce shifts in mixing regimes.

285

286 Two other shifts in mixing regime can also be expected with climate change, mediated
287 through changes in hydrology. In lakes where water level is projected to decrease with climate
288 change, a shift from stratified to polymictic can be expected if the water level falls below a

289 critical level to sustain seasonal stratification (Kirillin & Shatwell, 2016; Zohary &
290 Ostrovsky, 2011). Increase in water level could cause a shift in the opposite direction. Both
291 temperature and water level can be a driver of a shift between polymictic and stratified
292 regimes, and the feedbacks we discuss in the following section also apply to a shift driven by
293 water level change. In saline lakes a reduction of fresh water inflow can cause a shift from
294 meromictic to holomictic, as the freshwater layer on top of the heavier saline layer diminishes
295 (Gertman & Hecht, 2002; Kaden et al., 2010) and vice versa with an increase in precipitation
296 (Melack & Jellison, 1998). We are not aware of literature that describes feedbacks from the
297 new mixing regime to the hydrological input, or changed biogeochemical conditions under the
298 new regime that affect the vertical salt distribution in a way that affects the new regime's
299 stability. Our view is therefore that such a response of the saline lake mixing regime is a
300 direct function of the discharge and seasonality of the external inflow (although a threshold
301 response is possible), and because of the lack of known internal feedbacks, we will not treat
302 this regime shift further.

303

304 Shift from a polymictic to a seasonally stratified regime

305 Lakes of intermediate depth (\approx 5-10 m mean depth, Kirillin, 2010) can support both
306 polymictic and seasonally stratified (dimictic or monomictic) regimes, based on
307 morphometry, transparency, wind speed, and annual mean solar radiation flux (Kirillin &
308 Shatwell, 2016). A shift from polymixis to seasonal stratification might occur as a result of
309 climate warming in these lakes (Kirillin, 2010; Woolway & Merchant, 2019). This trend can
310 be amplified by reduced water transparency and lower wind speeds in summer (Shatwell et
311 al., 2016). If transparency is reduced, less energy penetrates to deeper layers, as more solar
312 radiation is absorbed near the surface. This can result in warming of the surface layer, cooling
313 of the hypolimnion, and overall stronger stratification (Jones et al., 2005; Tanentzap et al.,

314 2008), but the influence of transparency on stratification is significantly stronger in smaller
315 lakes due to a lower contribution of wind mixing to turbulence formation (Fee et al., 1996). A
316 decrease in transparency can be caused by phytoplankton growth or increased CDOM content,
317 for example as a consequence of catchment-based inflow of nutrients or organic matter.
318 CDOM loading from peatlands may increase as a function of climate change, for example
319 through increased decomposition at higher temperatures (Jennings et al., 2010). Wind is also a
320 crucial factor in exchanging heat between atmosphere and lakes by inducing mixing (Imboden
321 & Wüest, 1995), and can be a decisive factor for hypolimnetic temperature trends. Indeed,
322 decreasing wind speeds cause a cooling of the hypolimnion by reducing heat transfer to deep-
323 water layers (Magee & Wu, 2017). Regional trends in wind speed might have the potential to
324 cause a shift in mixing regimes (Woolway et al., 2019). However, wind forcing is an external
325 forcing to the lake system, and we are not aware of literature describing feedbacks between
326 wind forcing and lake conditions that reinforce either the polymictic or stratified mixing
327 regime.

328
329 Periods with warm and calm weather are promoted by climate change, and can induce long
330 stratification events in polymictic lakes, lasting multiple days or even weeks (Wilhelm &
331 Adrian, 2008). However, strong inter-annual variation in the duration of stratification within
332 the same lake has been documented, that cannot be explained by temperature changes alone
333 (Brothers et al., 2014; Riis & Sand-Jensen, 1998). Water transparency was determined to be a
334 major factor of shifts in mixing regime in the studies of Riis and Sand-Jensen (1998),
335 Brothers et al. (2014), and Shatwell et al. (2016), and is, as stated, influenced by
336 phytoplankton growth and CDOM content.

337

338 In this paper, we are interested in feedbacks that would stabilise a newly established stratified
339 regime, like mechanisms that would perpetuate lower transparency. Brothers et al. (2014)
340 described such a feedback, where strong rainfall flooded surrounding peatlands, leading to
341 increased CDOM and nutrient concentrations and higher water levels. Transparency was
342 reduced due to a combination of increased CDOM and phytoplankton, which caused
343 stratification and anoxia near the sediment, and promoted internal loading of CDOM and
344 nutrients from the sediment, stabilising the stratified state. For a different lake, Riis and Sand-
345 Jensen (1998) describe almost a doubling of the duration of stratification over a period of 40
346 years due to increased CDOM concentrations, but no stabilising feedbacks were identified.
347 Model simulations by Shatwell et al. (2016) suggested that phytoplankton can have a decisive
348 influence on mixing regimes in lakes of intermediate depth. The presence or absence of a
349 clear-water phase in spring could change the mixing regime for that year. No feedbacks are
350 described, however. Still, in shallow lakes a heatwave or period of calm can trigger a period
351 of stratification and potentially cause anoxia when oxygen depletion is sufficiently high,
352 followed by nutrient release to the photic zone when stratification ends (Wilhelm & Adrian,
353 2008). When the accumulated nutrients become available to phytoplankton during
354 stratification, for example due to buoyancy regulation, the ensuing bloom could reduce
355 transparency, leading to stronger heating of the upper water layers (Jones et al., 2005), and
356 thus stabilise the stratified regime.

357

358 However, despite the crucial role of transparency in regulating thermal stratification and the
359 study of Brothers et al. (2014) showing the potential of the transparency-reduction feedback
360 in environmental data, this feedback might only apply to a select set of lakes. Below, we give
361 three arguments why the likelihood that this feedback will cause bi-stability of polymixis and
362 seasonal stratification might be limited: 1) the feedback can regularly be overridden by

363 external perturbations unless a specific set of lake conditions, regarding morphometry and
364 transparency, is present, 2) stratification hinders exchange between sediment and surface
365 water, effectively weakening the feedback, and 3) there is a reset of lake conditions in winter
366 and no carry-on of the feedback to the next year.

367

368 The feedback requires a specific set of conditions to effectively influence lake mixing regime.
369 Lakes that are too shallow cannot sustain seasonal stratification as commonly recurring
370 convective or wind mixing events break down stratification completely. Conversely, deeper
371 lakes often already have a stratified regime, restricting bi-stability to lakes with an
372 intermediate depth range ($\approx 5 - 10$ m, Kirillin, 2010). In lakes larger than 5 km^2 , wind and
373 convective mixing are the decisive factors to determine the depth of stratification and
374 transparency only has a minor effect (Fee et al., 1996), so this feedback would only be
375 relevant in small lakes of intermediate depth. Persson and Jones (2008) show that in already
376 turbid water a change in transparency has little effect on thermal stability, which would
377 suggest that the transparency-reduction feedback requires an initially low turbidity. If all light
378 was absorbed in the mixed layer before the reduction of transparency, a further drop in
379 transparency would not make a large difference in heat distribution (Persson & Jones, 2008).
380 In the same line, a sensitivity analysis in the modelling study by Shatwell et al. (2019)
381 indicated that the effect of varying transparency on stratification is strongest in small lakes
382 with low to medium (up to approx. 1.0 m^{-1}) extinction coefficients.

383

384

385 Stratification restricts exchange of dissolved materials between deep and shallow water
386 layers. Therefore, sediment release of CDOM and nutrients would only marginally reach the
387 epilimnion and affect light penetration. Nutrients would reach the surface layer after a mixing

388 event, as is supported by findings of blooms after the end of stratification events (Wilhelm &
389 Adrian, 2008), but this would break the transparency-reduction feedback. Buoyant
390 cyanobacteria could – potentially - use the nutrients in the hypolimnion and move across the
391 thermocline into the light to grow (Paerl & Huisman, 2009), keeping the feedback loop intact.
392 In the study of Brothers et al. (2014), sediment release of substances did influence the pelagic
393 despite consistent stratification, but the role of the thermocline was not discussed. The
394 presence of a thermocline limits turbulence reaching the sediment, so stratification reduces
395 resuspension of particles that sink to the bottom, and promotes sedimentation losses.
396 Formation of stratification can thus reduce particle-based turbidity. The reduced turbidity in
397 turn decreases stratification, completing a negative feedback loop (Figure 2a). If the turbidity
398 is caused by sinking particles (e.g. non-buoyant phytoplankton cells), this negative feedback
399 inhibits sustenance of the stratified state.

400

401 Lastly, in winter, phytoplankton biomass is low and complete mixing occurs, so the feedback
402 loop is broken. Therefore, there is no carry-over of mixing regime from year to year. Years
403 with enhanced stratification could easily be followed by a year with polymictic behaviour
404 since the occurrence of seasonal stratification one year does not influence the likelihood of
405 stratification in the next year. Stratification can be triggered by a period of warm and calm
406 weather, which makes timing a relevant issue. A heatwave in spring/early summer can affect
407 the mixing regime for the rest of the year, but a similar event at the end of summer has only a
408 brief effect.

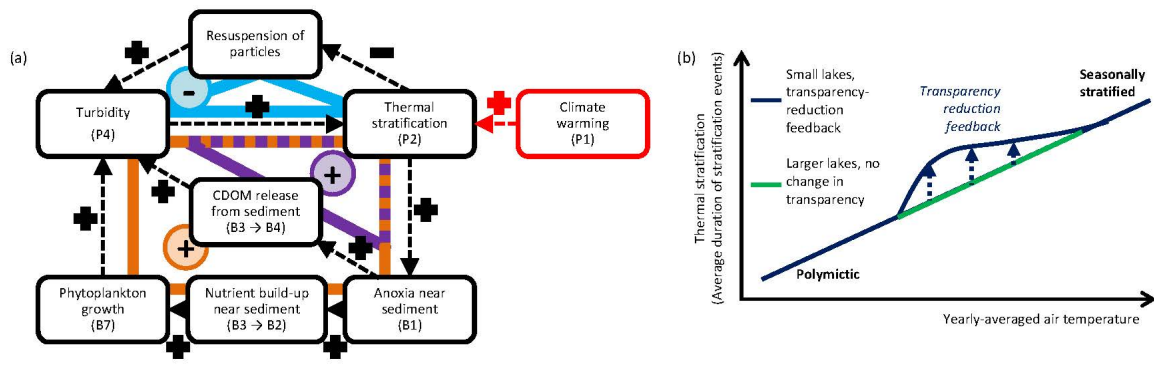
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410 [ENREF 7](#) [ENREF 100](#) [ENREF 116](#) [ENREF 86](#) [ENREF 101](#) Summarising, in a polymictic lake of
411 intermediate depth, a seasonally stratified regime can establish under lower wind speeds,
412 decreased transparency, or a higher water level (Kirillin & Shatwell, 2016). Changes in

413 transparency can strongly influence thermal stability (Persson & Jones, 2008; Tanentzap et
414 al., 2008), and even shift mixing regimes (Brothers et al., 2014; Shatwell et al., 2016).
415 Feedback loops could sustain the stratified state (Figure 2a), which might cause a sudden shift
416 from a polymictic to a seasonally stratified regime for a particular year (Figure 2b). However,
417 there is a suite of reasons why these feedbacks may not be dominant in most lakes.
418 Transparency changes only really affect thermal stratification in small, relatively clear lakes
419 of intermediate depth. Wind and cooling events can disturb stratification and interrupt the
420 feedback loop. Stratification hinders transport of sediment-released substances to the
421 epilimnion, which is a critical point in sustaining the feedback loop. Lastly, low
422 phytoplankton biomass and complete mixing in winter time prevent perpetuation of the
423 stratified state from one year to the next.

424
425 *Figure 2: a) The associated feedbacks for a shift from a polymictic to a seasonally stratified*
426 *regime. The effect of climate warming is shown in red. A reference to the corresponding*
427 *process in Figure 1 is given between brackets. Three feedback loops are formed. Both the*
428 *purple and the orange feedback loops are positive (i.e. self-reinforcing). The blue, negative*
429 *feedback loop activates when the turbidity that supports the stratification is caused by sinking*
430 *particles. b) State diagram of a shift from a polymictic lake of intermediate depth to a*
431 *seasonally stratified regime. Climate warming increases the duration of stratification events.*
432 *When these periods become long enough to trigger a reduction in transparency, in some years*
433 *there might be a sudden jump to a longer stratified period. This will most likely occur in small*
434 *lakes, where transparency has the strongest control on stratification patterns (blue line). If*
435 *the turbidity is caused by sinking particles, sedimentation of particles will likely result in*
436 *clearer water and the breakdown of stratification. In larger lakes, or lakes where the positive*
437 *feedbacks are only weak, the increase in duration of stratification will be more linear (green*

438 *line). In a seasonally stratified regime, a reduction in transparency will not, or only*
 439 *marginally, increase the length of the stratified period.*



440

441 Shift from a dimictic to a monomictic regime

442 Near the poles, loss of ice cover in deep lakes is likely to turn amictic lakes into cold
 443 monomictic lakes, and cold monomictic into dimictic lakes (Nöges et al., 2009). In temperate
 444 regions, it forces the two separate mixing events at the end of autumn and the end of spring
 445 into one period with a more-or-less uniform temperature profile; a shift from dimixis to
 446 monomixis (Arvola et al., 2009; Ficker et al., 2017).

447

448 For a freshwater lake of a given morphometry, weather conditions and water temperature
 449 determine whether ice forms or not (Leppäranta, 2015). Climate change drives the atmosphere
 450 towards warmer conditions, but due to natural variation in weather, perpetuation of ice-free
 451 conditions after one ice-free winter is unlikely unless water temperatures express a memory of
 452 previous winters. This memory might be established due to the large thermal heat capacity of
 453 deep lakes and a dominant effect of an ice-albedo. Ice has a higher albedo than water (i.e. ice
 454 reflects more shortwave radiation), reducing heating of an ice-covered lake. When ice
 455 disappears, the surface water warms faster through absorption of solar radiation (Austin &
 456 Colman, 2007). A modelling study on the Laurentian Great Lakes under a prescribed weather
 457 cycle, atmospheric noise, and slow climatic forcing, showed that ice in deep lakes can prevent
 458 lake warming by its high albedo and promotes ice cover in following years (Sugiyama et al.,

459 2017), which we define as a memory effect. Once ice disappeared, deep water layers warmed
460 up to a larger degree, making it harder for water temperature to reach freezing levels in
461 following years.

462
463 Only sufficiently deep lakes have sufficient thermal heat capacity to transfer the effect of ice
464 cover to the next winter; Sugiyama et al. (2017) investigated lakes with an average depth of at
465 least 50 metres, but do not give a minimum depth required to generate a memory effect. Bi-
466 stability occurred in ranges of annual mean air temperatures of ~ 0.5 °C (at 50 m depth) and
467 ~ 1.5 °C (at 150 m depth). Outside of these ranges, the lake was always ice-covered, or always
468 ice-free, regardless of the ice cover in previous winter. These ranges might be too narrow to
469 allow for observations, given the natural variability of the weather.

470
471 Apart from its higher albedo, ice insulates the lake from the atmosphere, limiting heat loss to
472 the atmosphere in winter (Leppäranta, 2015; Zhong et al., 2016). This insulation works in an
473 opposite direction as the ice-albedo feedback (Figure 3a), and it weakens the memory effect.
474 The relative importance of both processes is still disputed, but Sugiyama et al. (2017) find a
475 dominant ice-albedo feedback with a one- to three-column model. In contrast, at a higher
476 spatial resolution, Zhong et al. (2016) and Ye et al. (2018) did not find a dominant memory
477 effect and state that the role of ice albedo is small, suggesting a smoother transition from
478 dimictic to monomictic with a warming climate. All three modelling studies were performed
479 in a similar environment (the Great Lakes region) and actively investigated the role of ice-
480 albedo in determining thermal structure. Similarly, the modelling study of Shatwell et al.
481 (2019) reported a gradual shift from ice-covered to ice-free winters in two lakes of 20 to 30
482 metres mean depth in Europe, rather than an abrupt shift. Other studies on the ice-albedo
483 feedback and thermal memory in lakes are scarce. However, this topic has been addressed for

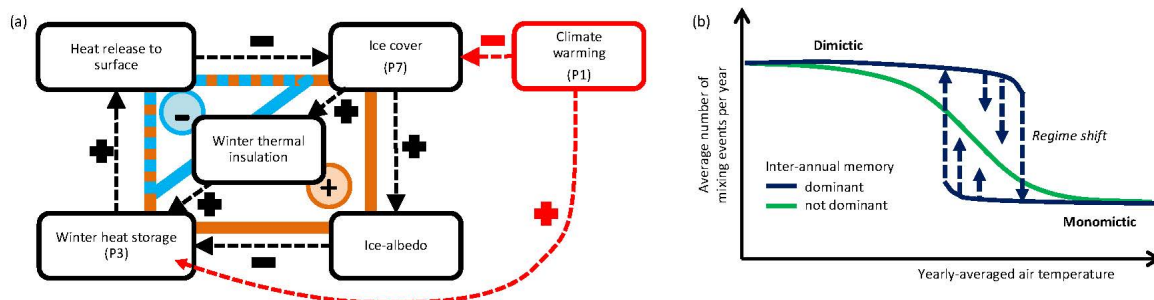
484 sea ice; modelling studies suggest that the response of sea ice to atmospheric temperature
485 changes might show lags, but is not truly bi-stable (Li et al., 2013; Ridley et al., 2012), and
486 therefore a gradual loss of ice cover is to be expected.

487

488 In brief, although the role of ice albedo in lakes is still debated, it is generally considered that
489 memory effects of ice cover in lakes have only a minor influence. In case of a dominant
490 memory effect, caused by a large thermal heat capacity and a dominant ice-albedo feedback,
491 shifts in mixing regime between monomictic and dimictic lakes would have a sudden nature
492 (Figure 3b, blue lines). If destabilising positive feedbacks are weak, a smoother transition
493 from monomictic to dimictic is expected, with alternating dimictic and monomictic years
494 (Figure 3b, green line). Both the ice-albedo feedback and the insulation effect could be
495 relevant for the shifts from amictic to cold monomictic and from cold monomictic to dimictic
496 as well. However, literature on these mixing regime shifts is limited.

497

498 *Figure 3: a) The associated feedbacks for a shift from a dimictic to a monomictic regime. The*
499 *effect of climate warming is shown in red. A reference to the corresponding process in Figure*
500 *1 is given between brackets. Two feedback loops are formed. The blue feedback loop is*
501 *negative (i.e. self-stabilising), while the orange loop is positive (self-reinforcing). b) State*
502 *diagram of a shift from a dimictic to a monomictic regime. Inter-annual thermal memory is*
503 *supported by a large heat storage capacity and the positive feedback in (a). In case of a*
504 *dominant memory effect, shifts in mixing regime would have a sudden nature (blue line and*
505 *arrows), while if the memory effect is not dominant (green line), there is a smoother*
506 *transition, with alternating dimictic and monomictic years. The length of the dotted arrows*
507 *denotes the probability of a regime shift from one mixing regime to another.*



508

509 Shift from a holomictic to an oligo- or meromictic regime

510 Some lakes that are (becoming) monomictic are experiencing less complete mixing events,
 511 and decreases in the maximum mixing depth (North et al., 2014; Saulnier-Talbot et al., 2014).
 512 Hydrodynamic models driven by climate scenarios predict this trend to continue, resulting in
 513 a progressively decreasing maximum mixing depth (Matzinger et al., 2007; Sahoo &
 514 Schladow, 2008; Schwefel et al., 2016). Complete mixing – i.e. top to bottom - can even
 515 disappear entirely and maximum mixing depth could decrease by up to 80% (Matzinger et al.,
 516 2007; Sahoo & Schladow, 2008). Perroud and Goyette (2010) predict a decrease in duration
 517 of fully mixed conditions for the peri-alpine Lake Geneva (Switzerland/France). These
 518 findings imply that complete mixing in monomictic lakes will decrease in the future and parts
 519 of the hypolimnion can stay isolated from the atmosphere for multiple years.

520

521 However, in oligomictic lakes there is an interplay between the increase in hypolimnetic
 522 temperature and the frequency of complete mixing events. The hypolimnion slowly heats over
 523 the year as a result of the geothermal heat flux and as warmer water from the epilimnion is
 524 gradually mixed into the deeper layers by turbulence. Incomplete winter mixing fails to cool
 525 the hypolimnion, resulting in a warming trend. This increase in hypolimnetic temperature
 526 facilitates complete mixing in subsequent years, as less cooling is required for an overturn.
 527 Additionally, the higher thermal expansivity of water at higher temperatures can increase the
 528 chance on complete mixing in lakes with elevated salt concentrations in the hypolimnion

529 (Matzinger et al., 2006). When deep mixing finally occurs during a colder winter,
530 hypolimnetic temperatures show a sudden drop and the resistance to full mixing in subsequent
531 years would increase again. This is why this process is referred to as a “sawtooth pattern”
532 (Livingstone, 1993; 1997). This pattern has been observed in several deep lakes (e.g. Coats et
533 al., 2006; Lepori & Roberts, 2015; Straile et al., 2003), and might facilitate sporadic overturn
534 events even under milder temperatures. Climate warming is predicted to lengthen the
535 warming periods and reduce the frequency of turnovers and subsequent cooling (Livingstone,
536 1997). In accordance with the sawtooth-pattern feedback, a decrease in the extent of winter
537 mixing is expected during ongoing climate warming. However, once a new plateau in air
538 temperatures is reached, frequency of complete mixing is likely to return to its previous level,
539 unless meromixis has formed.

540

541 In both oligomictic and meromictic lakes, oxygen replenishment in the hypolimnion is
542 strongly reliant on sporadically occurring winter mixing, and reduced frequency of overturns
543 means increased likelihood of anoxia (Foley et al., 2012; Schwefel et al., 2016). As model
544 predictions for Lake Tahoe (USA) show, anoxia can form even in clear and oligotrophic lakes
545 when deep-water mixing stops (Sahoo et al., 2013). As a secondary effect of this, internal
546 nutrient loading and harmful effects for lake productivity and fish can be expected as a lake
547 shifts from holomictic to oligomictic behaviour (O'Reilly et al., 2003). Internal loading in
548 stratifying lakes changes the distribution of nutrients in the system, by increasing the
549 concentration in the hypolimnion, but affecting the epilimnion only to a lesser extent. As
550 eutrophication also increases oxygen depletion, eutrophication and climate warming both
551 increase risk of anoxia.

552

553 Model studies of deep-water mixing predict a reduced frequency of complete turnovers or
554 even a complete disappearance, but as a gradual trend (Danis et al., 2004; Sahoo et al., 2013;
555 Schwefel et al., 2016). The sawtooth pattern of hypolimnetic temperatures in oligomictic
556 lakes facilitates deep mixing events after years with incomplete mixing (Livingstone, 1993).
557 However, most of the studies above did not include an effect of solutes (i.e. salinity) on water
558 density - a decisive factor in the formation of meromixis (Boehrer & Schultze, 2008;
559 Camacho et al., 2017). Meromictic lakes have a denser, chemically different water layer
560 below the hypolimnion, which is rarely mixed into the upper layers. Meromictic lakes can
561 behave strikingly differently from thermally stratified lakes in terms of temperature profile,
562 water renewal, chemistry, and ecology (Gulati et al., 2017; Lepori et al., 2018a). The causes
563 of meromixis are diverse (see Gulati et al., 2017), but a common characteristic is that the
564 density difference is sustained. For example, in case of high iron concentrations below an oxic
565 water layer, iron that is mixed into oxic water tends to precipitate and sink back into the
566 anoxic water, where it dissolves again and maintains the density stratification (Boehrer &
567 Schultze, 2008). Internal processes like this make meromixis generally a very stable mixing
568 regime.

569

570 Endogenic meromixis is a form of meromixis that is sustained by decomposition and
571 increased concentrations of dissolved substances by biogeochemical cycles in the deep water
572 layer (for full explanation, see Boehrer & Schultze, 2008). This leads to the hypothesis of
573 anoxia as a potential trigger for endogenic meromixis (Hutchinson, 1957; Julià et al., 1998).
574 In this situation, the onset of anoxia sets off the formation of a heavier water layer by an
575 increased build-up of solutes in the hypolimnion and complete mixing becomes too infrequent
576 to distribute these solutes through the water column. This build-up of solutes suppresses
577 further mixing and could cause a more abrupt and permanent formation of meromixis. In Lake

578 Lugano (Italy/Switzerland), endogenic meromixis might have formed as a result of
579 anthropogenic eutrophication (Lepori et al., 2018a). The possibility of meromixis caused by
580 climate change has not been addressed often in scientific literature. Julià et al. (1998) mention
581 endogenic meromixis as a potential cause of meromixis in the Spanish Lake La Cruz. In a
582 modelling study of the monomictic Lake Ohrid (North Macedonia/Albania), Matzinger et al.
583 (2007) found that above an atmospheric warming rate of 0.02 °C/yr, hypolimnetic
584 temperature increase would fall behind surface water warming rates. Additionally, solute
585 accumulation in the hypolimnion would further increase the density of deep waters,
586 preventing complete overturns in future scenarios (Matzinger et al., 2007). The increase in
587 solute concentration must be strong enough to offset a reduction of density by hypolimnetic
588 warming (Figure 4a). Several physical lake processes can mix surface water into the
589 hypolimnion, even when a chemical gradient is present, therefore reducing density
590 differences. Wind-induced internal waves increase turbulence around the thermocline, and
591 therefore mixing between both layers (Imboden & Wüest, 1995). Differential cooling is the
592 process where shallow areas experience fast convective cooling and this water mass moves
593 downwards along the lake slopes where morphology is suitable. This can lead to transport of
594 water from the surface to deep water layers (Ambrosetti et al., 2010; Peeters et al., 2003).
595 Intrusion of river inflow is another potentially important factor for deep-water renewal
596 (Ambrosetti et al., 2010). Depth of river intrusion depends amongst others on inflow water
597 temperature and lake thermal structure (Fink et al., 2016). High sediment densities in the
598 inflow can increase water density and allow penetration into the hypolimnion (Fink et al.,
599 2016; Loizeau & Dominik, 2000). Processes such as dam construction can reduce the
600 sediment density in inflows, and so decrease the deep-water renewal caused by inflows
601 (Loizeau & Dominik, 2000). In lakes where these processes cause significant deep-water
602 renewal, a shift to meromixis is less probable. Formation of meromixis due to climate

603 warming is also not likely in dimictic or polymictic lakes where complete mixing is frequent,
604 but could occur in monomictic lakes in multiple climate zones.

605

606 It is difficult to determine in which lakes a shift towards meromixis is most likely to occur.

607 Prime candidates are lakes that did not experience prolonged periods of anoxia and

608 incomplete mixing up to now, but are prone to experience these with the effects of climate

609 change. Especially deeper lakes seem to be vulnerable, due to their tendency to mix

610 incompletely (Danis et al., 2004). Yet these are not the only factors, as also the chemical

611 composition of the sediment and underlying bedrock determines the nature and quantity of

612 compounds that can be released under anoxic conditions (Boehrer & Schultze, 2008; Del Don

613 et al., 2001). Additionally, Matzinger et al. (2007) suggest that meromixis is stimulated under

614 a high rate of warming, which puts lakes at risk that lie in parts of the world that are

615 experiencing rapid warming. Altogether, the likelihood of formation of meromixis with

616 climate change is not obvious, and lake-specific approaches are necessary to evaluate this

617 risk. Modelling efforts such as the one by Matzinger et al. (2007) are a promising approach,

618 which should be supplemented by lake-specific information on sediment release rates of

619 major density-affecting solutes.

620

621 In summary, as a holomictic lake warms, the likelihood of incomplete mixing increases,

622 especially under fast warming rates (Matzinger et al., 2007). This creates an oligomictic

623 regime, where the sawtooth pattern (Livingstone, 1997) may result in complete mixing in

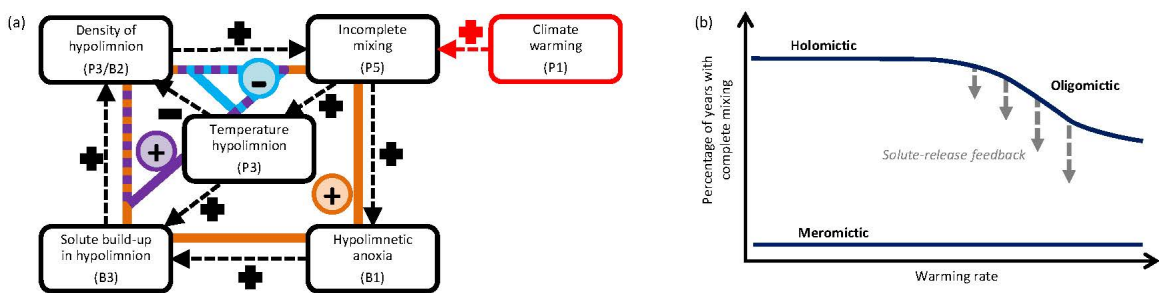
624 some years. This oligomictic regime increases the chance of anoxia and solute accumulation

625 in the hypolimnion, potentially culminating in a sudden shift to meromixis (Figure 4b). Once

626 a lake becomes meromictic, it might be difficult to revert its mixing regime (Lepori et al.,

2018a). Lakes with the potential of strong solute release from the sediment and weak deep-water renewal are most susceptible to such a shift.

Figure 4: a) The associated feedbacks for a shift from a holomictic to an oligo- or meromictic regime. The effect of climate warming is shown in red. A reference to the corresponding process in Figure 1 is given between brackets. The negative (self-stabilising) feedback loop, in blue, causes a decrease in the density of the hypolimnion after incomplete mixing, while the positive (self-reinforcing) feedback loops, in purple and orange, stimulate a density increase. b) State diagram of a shift from a holomictic to either an oligomictic or a meromictic regime. When incomplete mixing occurs as a result of warming, an oligomictic regime is formed. This increases the chances of forming anoxia and solute accumulation, potentially resulting in a meromictic regime if the density increase by solute build-up (positive feedbacks) exceeds the density decrease by hypolimnetic warming (negative feedback). The length of the dotted arrows denotes the probability of a regime shift from an oligomictic to a meromictic regime, but the possibility for this shift depends on lake-specific characteristics. A shift is most likely to occur in lakes with little deep-water renewal, where large quantities of solutes can be released from the sediment.



644
645 **Conclusion**

646 Climate change can cause shifts in the mixing regime of deep lakes, which will change their
647 behaviour in terms of physics, chemistry, and biology. In this study, we investigated whether

648 certain feedbacks can affect these regime shifts. The investigated potential shifts are from
649 polymictic to seasonally stratified, from dimictic to monomictic, and from holomictic to
650 oligo- or meromictic. All these shifts in mixing regime display reinforcing feedback
651 mechanisms, but these feedbacks are likely to be relevant under certain conditions only. In
652 lakes of intermediate depth, polymixis and seasonal stratification can be alternative states,
653 based on transparency and wind sheltering. If a period of stratification can trigger a strong
654 reduction in transparency, for example due to phytoplankton bloom formation or release of
655 CDOM, a stratified regime can form. However, this feedback is valid only under a narrow
656 range of lake conditions, and the stratified state is not carried-over from year to year, with a
657 full reset in each new year. Dimictic lakes can become monomictic due to loss of ice cover.
658 One study found that a shift from dimixis to monomixis could show bi-stability because of the
659 ice-albedo feedback coupled to thermal heat capacity in sufficiently deep lakes, but other
660 studies in lakes and the sea suggest the opposite. The majority of studies would predict only a
661 minor influence of memory effect of ice cover on lake dynamics, and therefore a gradual shift
662 from mostly ice-covered to mostly ice-free winters. A climate-induced shift from holomixis to
663 meromixis can occur if a density increase of the deep water layer by solute build-up
664 outweighs a density decrease due to hypolimnetic warming. Such a shift would have profound
665 influences on aquatic ecosystems, but more research is needed on this topic to assess where
666 and when this can happen. If incomplete mixing does not result in a net density increase of the
667 deep waters, an oligomictic regime is formed.

668

669 Although climate, interannual temperature variation, and morphometry are the main
670 determinants of a mixing regime, transparency, water level, and internal feedbacks can
671 facilitate and stabilise shifts between mixing regimes. Without denying the value of studies
672 investigating mixing regime shifts driven by warming alone, we hope this paper places those

673 findings in the perspective that several other components of lake ecosystems can influence
674 mixing regimes as well. A change in mixing regime can mean a step-change in a physico-
675 chemical parameter (e.g. anoxia) that can feed back to the vertical density distribution or heat
676 budget. If we consider these processes as well, we may get a better understanding of how
677 climate change affects lake mixing regimes. Given the great importance of mixing regime for
678 functioning of lakes, more knowledge on the likelihood of transitions and the stability of such
679 changes would be important for lake management. Observations of shifts in mixing regime
680 due to internal lake processes are important, but may be hard to realise due to the long
681 timescales and required data involved. For each of the three mixing regime shifts studied in
682 this paper, modelling approaches have done important findings. Inclusion of biogeochemistry
683 in modelling could lead to further advances when investigating the shifts polymictic-stratified
684 and holomictic-meromictic. The study of feedback loops in lake processes, has so far been
685 focussed mainly on shallow lakes (e.g. Scheffer, 1998). Our review is one of the first studies
686 to systematically explore the potential feedbacks occurring in deep lakes, as well as the
687 climate dependency of these mechanisms.

688

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692 **References**

- 693 Adrian, R., O'Reilly, C. M., Zagarese, H., Baines, S. B., Hessen, D. O., Keller, W., . . . Winder, M. (2009).
 694 Lakes as sentinels of climate change. *Limnology and Oceanography*, *54*(6 part 2), 2283-2297.
 695 doi:10.4319/lo.2009.54.6_part_2.2283
- 696 Allott, N. A. (1986). Temperature, oxygen and heat-budgets of six small western Irish lakes.
 697 *Freshwater Biology*, *16*(2), 145-154. doi:10.1111/j.1365-2427.1986.tb00959.x
- 698 Ambrosetti, W., Barbanti, L., & Carrara, E. A. (2010). Mechanisms of hypolimnion erosion in a deep
 699 lake (Lago Maggiore, N. Italy). *Journal of Limnology*, *69*(1), 3-14. doi:10.4081/jlimnol.2010.3
- 700 Arvola, L., George, G., Livingstone, D. M., Järvinen, M., Blenckner, T., Dokulil, M. T., . . .
 701 Weyhenmeyer, G. A. (2009). The Impact of the Changing Climate on the Thermal
 702 Characteristics of Lakes. In G. George (Ed.), *The Impact of Climate Change on European Lakes*
 703 (pp. 85-101).
- 704 Austin, J. A., & Colman, S. M. (2007). Lake Superior summer water temperatures are increasing more
 705 rapidly than regional air temperatures: A positive ice-albedo feedback. *Geophysical Research*
 706 *Letters*, *34*(6), L06604. doi:10.1029/2006gl029021
- 707 Boehrer, B., & Schultze, M. (2008). Stratification of lakes. *Reviews of Geophysics*, *46*(2),
 708 2006RG000210. doi:10.1029/2006rg000210
- 709 Boehrer, B., von Rohden, C., & Schultze, M. (2017). Physical features of meromictic lakes:
 710 Stratification and circulation. In R. D. Gulati, E. S. Zadereev, & A. G. Degermendzhi (Eds.),
 711 *Ecology of Meromictic Lakes* (pp. 15-34): Springer.
- 712 Brothers, S., Köhler, J., Attermeyer, K., Grossart, H.-P., Mehner, T., Meyer, N., . . . Hilt, S. (2014). A
 713 feedback loop links brownification and anoxia in a temperate, shallow lake. *Limnology and*
 714 *Oceanography*, *59*(4), 1388-1398. doi:10.4319/lo.2014.59.4.1388
- 715 Camacho, A., Miracle, M. R., Romero-Viana, L., Picazo, A., & Vicente, E. (2017). Lake La Cruz, an iron-
 716 rich karstic meromictic lake in Central Spain. In R. D. Gulati, E. S. Zadereev, & A. G.
 717 Degermendzhi (Eds.), *Ecology of Meromictic Lakes* (pp. 187-233): Springer.
- 718 Coats, R., Perez-Losada, J., Schladow, G., Richards, R., & Goldman, C. (2006). The warming of lake
 719 Tahoe. *Climatic Change*, *76*(1), 121-148. doi:10.1007/s10584-005-9006-1
- 720 Crockford, L., Jordan, P., Melland, A., & Taylor, D. (2015). Storm-triggered, increased supply of
 721 sediment-derived phosphorus to the epilimnion in a small freshwater lake. *Inland Waters*,
 722 *5*(1), 15-26. doi:10.5268/iw-5.1.738
- 723 Danis, P.-A., von Grafenstein, U., Masson-Delmotte, V., Planton, S., Gerdeaux, D., & Moisselin, J. M.
 724 (2004). Vulnerability of two European lakes in response to future climatic changes.
 725 *Geophysical Research Letters*, *31*(21), L21507. doi:10.1029/2004gl020833
- 726 De Brabandere, L., Bonaglia, S., Kononets, M. Y., Viktorsson, L., Stigebrandt, A., Thamdrup, B., & Hall,
 727 P. O. J. (2015). Oxygenation of an anoxic fjord basin strongly stimulates benthic
 728 denitrification and DNRA. *Biogeochemistry*, *126*(1-2), 131-152. doi:10.1007/s10533-015-
 729 0148-6
- 730 Del Don, C., Hanselmann, K. W., Peduzzi, R., & Bachofen, R. (2001). The meromictic alpine Lake
 731 Cadagno: orographical and biogeochemical description. *Aquatic Sciences*, *63*(1), 70-90.
 732 doi:10.1007/PL00001345
- 733 Diehl, S., Berger, S., Ptacnik, R., & Wild, A. (2002). Phytoplankton, light, and nutrients in a gradient of
 734 mixing depths: field experiments. *Ecology*, *83*(2), 399-411. doi:10.1890/0012-
 735 9658(2002)083[0399:PLANIA]2.0.CO;2
- 736 Doubek, J. P., Campbell, K. L., Doubek, K. M., Hamre, K. D., Lofton, M. E., McClure, R. P., . . . Carey, C.
 737 C. (2018). The effects of hypolimnetic anoxia on the diel vertical migration of freshwater
 738 crustacean zooplankton. *Ecosphere*, *9*(7), e02332. doi:doi:10.1002/ecs2.2332
- 739 Fang, X., & Stefan, H. G. (1999). Projections of climate change effects on water temperature
 740 characteristics of small lakes in the contiguous US. *Climatic Change*, *42*(2), 377-412.
 741 doi:10.1023/A:1005431523281

742 Fang, X., & Stefan, H. G. (2009). Simulations of climate effects on water temperature, dissolved
743 oxygen, and ice and snow covers in lakes of the contiguous US under past and future climate
744 scenarios. *Limnology and Oceanography*, *54*(6 part 2), 2359-2370.
745 doi:10.4319/lo.2009.54.6_part_2.2359

746 Fee, E. J. (1976). The vertical and seasonal distribution of chlorophyll in lakes of the Experimental
747 Lakes Area, northwestern Ontario: Implications for primary production estimates. *Limnology
748 and Oceanography*, *21*(6), 767-783. doi:10.4319/lo.1976.21.6.0767

749 Fee, E. J., Hecky, R. E., Kasian, S. E. M., & Cruikshank, D. R. (1996). Effects of lake size, water clarity,
750 and climatic variability on mixing depths in Canadian Shield lakes. *Limnology and
751 Oceanography*, *41*(5), 912-920. doi:10.4319/lo.1996.41.5.0912

752 Ficker, H., Luger, M., & Gassner, H. (2017). From dimictic to monomictic: Empirical evidence of
753 thermal regime transitions in three deep alpine lakes in Austria induced by climate change.
754 *Freshwater Biology*, *62*(8), 1335-1345. doi:10.1111/fwb.12946

755 Fink, G., Wessels, M., & Wüest, A. (2016). Flood frequency matters: Why climate change degrades
756 deep-water quality of peri-alpine lakes. *Journal of Hydrology*, *540*, 457-468.
757 doi:10.1016/j.jhydrol.2016.06.023

758 Foley, B., Jones, I. D., Maberly, S. C., & Rippey, B. (2012). Long-term changes in oxygen depletion in a
759 small temperate lake: effects of climate change and eutrophication. *Freshwater Biology*,
760 *57*(2), 278-289. doi:10.1111/j.1365-2427.2011.02662.x

761 Forel, F. A. (1880). Températures lacustres. Recherches sur la température du lac Léman et d'autres
762 lacs d'eau douce. *Archives des Sciences physiques et naturelles de Genève*, *3*, 501-515.

763 Friedrich, J., Janssen, F., Aleynik, D., Bange, H. W., Boltacheva, N., Çagatay, M. N., . . . Wenzhöfer, F.
764 (2014). Investigating hypoxia in aquatic environments: diverse approaches to addressing a
765 complex phenomenon. *Biogeosciences*, *11*(4), 1215-1259. doi:10.5194/bg-11-1215-2014

766 Fukushima, T., Matsushita, B., Subehi, L., Setiawan, F., & Wibowo, H. (2017). Will hypolimnetic
767 waters become anoxic in all deep tropical lakes? *Scientific Reports*, *7*, 45320.
768 doi:10.1038/srep45320

769 Gertman, I., & Hecht, A. (2002). The Dead Sea hydrography from 1992 to 2000. *Journal of marine
770 systems*, *35*(3-4), 169-181. doi:10.1016/S0924-7963(02)00079-9

771 Giling, D. P., Nejstgaard, J. C., Berger, S. A., Grossart, H. P., Kirillin, G., Penske, A., . . . Gessner, M. O.
772 (2017a). Thermocline deepening boosts ecosystem metabolism: evidence from a large-scale
773 lake enclosure experiment simulating a summer storm. *Global change biology*, *23*(4), 1448-
774 1462. doi:10.1111/gcb.13512

775 Giling, D. P., Staehr, P. A., Grossart, H. P., Andersen, M. R., Boehrer, B., Escot, C., . . . Obrador, B.
776 (2017b). Delving deeper: Metabolic processes in the metalimnion of stratified lakes.
777 *Limnology and Oceanography*, *62*(3), 1288-1306. doi:10.1002/lno.10504

778 Grasset, C., Mendonça, R., Villamor Saucedo, G., Bastviken, D., Roland, F., & Sobek, S. (2018). Large
779 but variable methane production in anoxic freshwater sediment upon addition of
780 allochthonous and autochthonous organic matter. *Limnology and Oceanography*, *63*(4),
781 1488-1501. doi:10.1002/lno.10786

782 Gudasz, C., Bastviken, D., Steger, K., Premke, K., Sobek, S., & Tranvik, L. J. (2010). Temperature-
783 controlled organic carbon mineralization in lake sediments. *Nature*, *466*(7305), 478-481.
784 doi:10.1038/nature09186

785 Gulati, R. D., Zadereev, E. S., & Degermendzhi, A. G. (2017). *Ecology of Meromictic Lakes* (Vol. 228):
786 Springer.

787 Hamilton-Taylor, J., Davison, W., & Morfett, K. (1996). The biogeochemical cycling of Zn, Cu, Fe, Mn,
788 and dissolved organic C in a seasonally anoxic lake. *Limnology and Oceanography*, *41*(3), 408-
789 418. doi:10.4319/lo.1996.41.3.0408

790 Hobbs, W. O., Hobbs, J. M. R., LaFrançois, T., Zimmer, K. D., Theissen, K. M., Edlund, M. B., . . .
791 Carlson, T. J. (2012). A 200-year perspective on alternative stable state theory and lake
792 management from a biomanipulated shallow lake. *Ecological Applications*, *22*(5), 1483-1496.
793 doi:10.1890/11-1485.1

794 Huisman, J., Sharples, J., Stroom, J. M., Visser, P. M., Kardinaal, W. E. A., Verspagen, J. M., &
795 Sommeijer, B. (2004). Changes in turbulent mixing shift competition for light between
796 phytoplankton species. *Ecology*, *85*(11), 2960-2970. doi:10.1890/03-0763
797 Huisman, J., van Oostveen, P., & Weissing, F. J. (1999). Critical depth and critical turbulence: two
798 different mechanisms for the development of phytoplankton blooms. *Limnology and*
799 *Oceanography*, *44*(7), 1781-1787. doi:10.4319/lo.1999.44.7.1781
800 Hupfer, M., & Lewandowski, J. (2008). Oxygen Controls the Phosphorus Release from Lake Sediments
801 - a Long-Lasting Paradigm in Limnology. *International Review of Hydrobiology*, *93*(4-5), 415-
802 432. doi:10.1002/iroh.200711054
803 Hutchinson, G. E. (1957). *A Treatise on Limnology* (Vol. 1). New York, USA: Wiley.
804 Hutchinson, G. E., & Löffler, H. (1956). The thermal classification of lakes. *Proceedings of the National*
805 *Academy of Sciences*, *42*(2), 84-86.
806 Hutter, K., & Jöhnk, K. (2004). *Continuum methods of physical modeling: continuum mechanics,*
807 *dimensional analysis, turbulence*: Springer Science & Business Media.
808 Ibelings, B. W., Portielje, R., Lammens, E. H. R. R., Noordhuis, R., van den Berg, M. S., Jooisse, W., &
809 Meijer, M. L. (2007). Resilience of Alternative Stable States during the Recovery of Shallow
810 Lakes from Eutrophication: Lake Veluwe as a Case Study. *Ecosystems*, *10*(1), 4-16.
811 doi:10.1007/s10021-006-9009-4
812 Idso, S. B. (1973). On the concept of lake stability. *Limnology and Oceanography*, *18*(4), 681-683.
813 doi:10.4319/lo.1973.18.4.0681
814 Imboden, D. M., & Wüest, A. (1995). Mixing mechanisms in lakes. In A. Lerman, D. M. Imboden, & J.
815 R. Gat (Eds.), *Physics and chemistry of lakes* (pp. 83-138): Springer.
816 IPCC. (2014). *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to*
817 *the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Retrieved
818 from IPCC, Geneva, Switzerland:
819 Ito, Y., & Momii, K. (2015). Impacts of regional warming on long-term hypolimnetic anoxia and
820 dissolved oxygen concentration in a deep lake. *Hydrological processes*, *29*(9), 2232-2242.
821 doi:10.1002/hyp.10362
822 Janssen, A. B. G., Teurlincx, S., An, S., Janse, J. H., Paerl, H. W., & Mooij, W. M. (2014). Alternative
823 stable states in large shallow lakes? *Journal of Great Lakes Research*, *40*(4), 813-826.
824 doi:10.1016/j.jglr.2014.09.019
825 Jansson, M., Blomqvist, P., Jonsson, A., & Bergström, A. K. (1996). Nutrient limitation of
826 bacterioplankton, autotrophic and mixotrophic phytoplankton, and heterotrophic
827 nanoflagellates in Lake Öträsket. *Limnology and Oceanography*, *41*(7), 1552-1559.
828 doi:10.4319/lo.1996.41.7.1552
829 Järvalt, A., Krause, T., & Palm, A. (2005). Diel migration and spatial distribution of fish in a small
830 stratified lake. In *Lake Verevi, Estonia—A Highly Stratified Hypertrophic Lake* (pp. 197-203):
831 Springer.
832 Jennings, E., Järvinen, M., Allott, N., Arvola, L., Moore, K., Naden, P., . . . Weyhenmeyer, G. A. (2010).
833 Impacts of climate on the flux of dissolved organic carbon from catchments. In G. George
834 (Ed.), *The Impact of Climate Change on European Lakes* (pp. 199-220): Springer.
835 Jennings, E., Jones, S., Arvola, L., Staehr, P. A., Gaiser, E., Jones, I. D., . . . De Eyto, E. (2012). Effects of
836 weather-related episodic events in lakes: an analysis based on high-frequency data.
837 *Freshwater Biology*, *57*(3), 589-601. doi:10.1111/j.1365-2427.2011.02729.x
838 Jöhnk, K. D., Huisman, J., Sharples, J., Sommeijer, B., Visser, P. M., & Stroom, J. M. (2008). Summer
839 heatwaves promote blooms of harmful cyanobacteria. *Global change biology*, *14*(3), 495-
840 512. doi:10.1111/j.1365-2486.2007.01510.x
841 Jones, I., George, G., & Reynolds, C. (2005). Quantifying effects of phytoplankton on the heat budgets
842 of two large limnetic enclosures. *Freshwater Biology*, *50*(7), 1239-1247. doi:10.1111/j.1365-
843 2427.2005.01397.x

844 Julià, R., Burjachs, F., Dasí, M. J., Mezquita, F., Miracle, M. R., Roca, J. R., . . . Vicente, E. (1998).
845 Meromixis origin and recent trophic evolution in the Spanish mountain lake La Cruz. *Aquatic*
846 *Sciences*, 60(4), 279-299. doi:10.1007/s000270050042

847 Kaden, H., Peeters, F., Lorke, A., Kipfer, R., Tomonaga, Y., & Karabiyikoglu, M. (2010). Impact of lake
848 level change on deep-water renewal and oxic conditions in deep saline Lake Van, Turkey.
849 *Water Resources Research*, 46(11). doi:10.1029/2009wr008555

850 Kirillin, G. (2010). Modeling the impact of global warming on water temperature and seasonal mixing
851 regimes in small temperate lakes. *Boreal environment research*, 15(2), 279-293.

852 Kirillin, G., & Shatwell, T. (2016). Generalized scaling of seasonal thermal stratification in lakes. *Earth-*
853 *Science Reviews*, 161, 179-190. doi:10.1016/j.earscirev.2016.08.008

854 Kraemer, B. M., Anneville, O., Chandra, S., Dix, M., Kuusisto, E., Livingstone, D. M., . . . McIntyre, P. B.
855 (2015). Morphometry and average temperature affect lake stratification responses to climate
856 change. *Geophysical Research Letters*, 42(12), 4981-4988. doi:10.1002/2015GL064097

857 Kraemer, B. M., Mehner, T., & Adrian, R. (2017). Reconciling the opposing effects of warming on
858 phytoplankton biomass in 188 large lakes. *Scientific Reports*, 7(1), 10762.
859 doi:10.1038/s41598-017-11167-3

860 Kreling, J., Bravidor, J., McGinnis, D. F., Koschorreck, M., & Lorke, A. (2014). Physical controls of
861 oxygen fluxes at pelagic and benthic oxyclines in a lake. *Limnology and Oceanography*, 59(5),
862 1637-1650. doi:10.4319/lo.2014.59.5.1637

863 Kuha, J., Arvola, L., Hanson, P. C., Huotari, J., Huttula, T., Juntunen, J., . . . Karjalainen, J. (2016).
864 Response of boreal lakes to episodic weather-induced events. *Inland Waters*, 6(4), 523-534.
865 doi:10.1080/IW-6.4.886

866 Lam, D. C. L., Schertzer, W. M., & Fraser, A. S. (1987). Oxygen depletion in Lake Erie: modeling the
867 physical, chemical, and biological interactions, 1972 and 1979. *Journal of Great Lakes*
868 *Research*, 13(4), 770-781. doi:10.1016/S0380-1330(87)71690-6

869 Lehmann, M. F., Simona, M., Wyss, S., Blees, J., Frame, C. H., Niemann, H., . . . Zopfi, J. (2015).
870 Powering up the “biogeochemical engine”: the impact of exceptional ventilation of a deep
871 meromictic lake on the lacustrine redox, nutrient, and methane balances. *Frontiers in Earth*
872 *Science*, 3, 45. doi:10.3389/feart.2015.00045

873 Lepori, F., Bartosiewicz, M., Simona, M., & Veronesi, M. (2018a). Effects of winter weather and
874 mixing regime on the restoration of a deep perialpine lake (Lake Lugano, Switzerland and
875 Italy). *Hydrobiologia*, 824(1), 229-242. doi:10.1007/s10750-018-3575-2

876 Lepori, F., & Roberts, J. J. (2015). Past and future warming of a deep European lake (Lake Lugano):
877 What are the climatic drivers? *Journal of Great Lakes Research*, 41(4), 973-981.
878 doi:10.1016/j.jglr.2015.08.004

879 Lepori, F., Roberts, J. J., & Schmidt, T. S. (2018b). A paradox of warming in a deep peri-Alpine lake
880 (Lake Lugano, Switzerland and Italy). *Hydrobiologia*, 824(1), 215-228. doi:10.1007/s10750-
881 018-3649-1

882 Leppäranta, M. (2015). *Freezing of lakes and the evolution of their ice cover*: Springer Science &
883 Business Media.

884 Lewis Jr, W. M. (1973). The Thermal Regime Of Lake Lanao (Philippines) And Its Theoretical
885 Implications For Tropical Lakes 1. *Limnology and Oceanography*, 18(2), 200-217.
886 doi:10.4319/lo.1973.18.2.0200

887 Lewis Jr, W. M. (1983). A revised classification of lakes based on mixing. *Canadian Journal of Fisheries*
888 *and Aquatic Sciences*, 40(10), 1779-1787. doi:10.1139/f83-207

889 Lewis Jr, W. M. (1996). Tropical lakes: How latitude makes a difference. In S. Academic (Ed.),
890 *Perspectives Tropical Limnology*. Amsterdam: SPB Academic.

891 Li, C., Notz, D., Tietsche, S., & Marotzke, J. (2013). The Transient versus the Equilibrium Response of
892 Sea Ice to Global Warming. *Journal of Climate*, 26(15), 5624-5636. doi:10.1175/jcli-d-12-
893 00492.1

894 Livingstone, D. M. (1993). Temporal structure in the deep-water temperature of four Swiss lakes: A
895 short-term climatic change indicator? *Internationale Vereinigung für theoretische und*

896 *angewandte Limnologie: Verhandlungen*, 25(1), 75-81.
897 doi:10.1080/03680770.1992.11900062

898 Livingstone, D. M. (1997). An example of the simultaneous occurrence of climate-driven “sawtooth”
899 deep-water warming/cooling episodes in several Swiss lakes. *Internationale Vereinigung für*
900 *theoretische und angewandte Limnologie: Verhandlungen*, 26(2), 822-828.
901 doi:10.1080/03680770.1995.11900832

902 Livingstone, D. M. (2008). A change of climate provokes a change of paradigm: taking leave of two
903 tacit assumptions about physical lake forcing. *International Review of Hydrobiology*, 93(4-5),
904 404-414. doi:10.1002/iroh.200811061

905 Loizeau, J.-L., & Dominik, J. (2000). Evolution of the Upper Rhone River discharge and suspended
906 sediment load during the last 80 years and some implications for Lake Geneva. *Aquatic*
907 *Sciences*, 62(1), 54-67. doi:10.1007/s000270050075

908 Mackay, E. B., Folkard, A. M., & Jones, I. D. (2014). Interannual variations in atmospheric forcing
909 determine trajectories of hypolimnetic soluble reactive phosphorus supply in a eutrophic
910 lake. *Freshwater Biology*, 59(8), 1646-1658. doi:10.1111/fwb.12371

911 Magee, M. R., & Wu, C. H. (2017). Response of water temperatures and stratification to changing
912 climate in three lakes with different morphometry. *Hydrology and Earth System Sciences*,
913 21(12), 6253-6274. doi:10.5194/hess-21-6253-2017

914 Matzinger, A., Schmid, M., Veljanoska-Sarafiloska, E., Patceva, S., Guseska, D., Wagner, B., . . . Wüest,
915 A. (2007). Eutrophication of ancient Lake Ohrid: Global warming amplifies detrimental effects
916 of increased nutrient inputs. *Limnology and Oceanography*, 52(1), 338-353.
917 doi:10.4319/lo.2007.52.1.0338

918 Matzinger, A., Spirkovski, Z., Patceva, S., & Wüest, A. (2006). Sensitivity of ancient Lake Ohrid to local
919 anthropogenic impacts and global warming. *Journal of Great Lakes Research*, 32(1), 158-179.
920 doi:10.3394/0380-1330(2006)32[158:SOALOT]2.0.CO;2

921 Melack, J. M., & Jellison, R. (1998). Limnological conditions in Mono Lake: contrasting monomixis and
922 meromixis in the 1990s. *Hydrobiologia*, 384(1-3), 21-39. doi:10.1023/A:1003352511328

923 Mischke, U. (2003). Cyanobacteria associations in shallow polytrophic lakes: influence of
924 environmental factors. *Acta Oecologica*, 24, S11-S23. doi:10.1016/S1146-609X(03)00003-1

925 Müller, B., Bryant, L. D., Matzinger, A., & Wüest, A. (2012). Hypolimnetic oxygen depletion in
926 eutrophic lakes. *Environmental science & technology*, 46(18), 9964-9971.
927 doi:10.1021/es301422r

928 Nöges, T., Nöges, P., Jolma, A., & Kaitaranta, J. (2009). *Impacts of climate change on physical*
929 *characteristics of lakes in Europe*. Retrieved from

930 North, R. P., North, R. L., Livingstone, D. M., Köster, O., & Kipfer, R. (2014). Long-term changes in
931 hypoxia and soluble reactive phosphorus in the hypolimnion of a large temperate lake:
932 consequences of a climate regime shift. *Global change biology*, 20(3), 811-823.
933 doi:10.1111/gcb.12371

934 O'Reilly, C. M., Alin, S. R., Plisnier, P.-D., Cohen, A. S., & McKee, B. A. (2003). Climate change
935 decreases aquatic ecosystem productivity of Lake Tanganyika, Africa. *Nature*, 424(6950),
936 766-768. doi:10.1038/nature01833

937 O'Reilly, C. M., Sharma, S., Gray, D. K., Hampton, S. E., Read, J. S., Rowley, R. J., . . . Zhang, G. (2015).
938 Rapid and highly variable warming of lake surface waters around the globe. *Geophysical*
939 *Research Letters*, 42(24), 10,773-710,781. doi:10.1002/2015gl066235

940 Obrador, B., Staehr, P. A., & Christensen, J. P. C. (2014). Vertical patterns of metabolism in three
941 contrasting stratified lakes. *Limnology and Oceanography*, 59(4), 1228-1240.
942 doi:10.4319/lo.2014.59.4.1228

943 Padišák, J., & Reynolds, C. S. (2003). Shallow lakes: the absolute, the relative, the functional and the
944 pragmatic. *Hydrobiologia*, 506(1-3), 1-11. doi:10.1023/B:HYDR.0000008630.49527.29

945 Paerl, H. W., & Huisman, J. (2009). Climate change: a catalyst for global expansion of harmful
946 cyanobacterial blooms. *Environmental Microbiology Reports*, 1(1), 27-37. doi:10.1111/j.1758-
947 2229.2008.00004.x

948 Peeters, F., Finger, D., Hofer, M., Brennwald, M., Livingstone, D. M., & Kipfer, R. (2003). Deep-water
949 renewal in Lake Issyk-Kul driven by differential cooling. *Limnology and Oceanography*, *48*(4),
950 1419-1431. doi:10.4319/lo.2003.48.4.1419

951 Peeters, F., Livingstone, D. M., Goudsmit, G.-H., Kipfer, R., & Forster, R. (2002). Modeling 50 years of
952 historical temperature profiles in a large central European lake. *Limnology and*
953 *Oceanography*, *47*(1), 186-197. doi:10.4319/lo.2002.47.1.0186

954 Perroud, M., & Goyette, S. (2010). Impacts of warmer climate on Lake Geneva water-temperature
955 profiles. *Boreal environment research*, *15*, 255-278.

956 Persson, I., & Jones, I. D. (2008). The effect of water colour on lake hydrodynamics: a modelling
957 study. *Freshwater Biology*, *53*(12), 2345-2355. doi:10.1111/j.1365-2427.2008.02049.x

958 Ravens, T. M., Kocsis, O., Wüest, A., & Granin, N. (2000). Small-scale turbulence and vertical mixing in
959 Lake Baikal. *Limnology and Oceanography*, *45*(1), 159-173. doi:10.4319/lo.2000.45.1.0159

960 Ridley, J. K., Lowe, J. A., & Hewitt, H. T. (2012). How reversible is sea ice loss? *The Cryosphere*, *6*(1),
961 193-198. doi:10.5194/tc-6-193-2012

962 Riis, T., & Sand-Jensen, K. (1998). Development of vegetation and environmental conditions in an
963 oligotrophic Danish lake over 40 years. *Freshwater Biology*, *40*(1), 123-134.
964 doi:10.1046/j.1365-2427.1998.00338.x

965 Rippey, B., & McSorley, C. (2009). Oxygen depletion in lake hypolimnia. *Limnology and*
966 *Oceanography*, *54*(3), 905-916. doi:10.4319/lo.2009.54.3.0905

967 Sahoo, G. B., & Schladow, S. G. (2008). Impacts of climate change on lakes and reservoirs dynamics
968 and restoration policies. *Sustainability Science*, *3*(2), 189-199. doi:10.1007/s11625-008-0056-
969 y

970 Sahoo, G. B., Schladow, S. G., Reuter, J. E., Coats, R., Dettinger, M., Riverson, J., . . . Costa-Cabral, M.
971 (2013). The response of Lake Tahoe to climate change. *Climatic Change*, *116*(1), 71-95.
972 doi:10.1007/s10584-012-0600-8

973 Saulnier-Talbot, É., Gregory-Eaves, I., Simpson, K. G., Efitre, J., Nowlan, T. E., Taranu, Z. E., &
974 Chapman, L. J. (2014). Small changes in climate can profoundly alter the dynamics and
975 ecosystem services of tropical crater lakes. *PloS one*, *9*(1), e86561.
976 doi:10.1371/journal.pone.0086561

977 Scheffer, M. (1998). *Ecology of Shallow Lakes*. London: Chapman & Hall.

978 Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walker, B. (2001). Catastrophic shifts in
979 ecosystems. *Nature*, *413*(6856), 591. doi:10.1038/35098000

980 Schmid, M., Tietze, K., Halbwachs, M., Lorke, A., McGinnis, D. F., & Wüest, A. (2002). How hazardous
981 is the gas accumulation in Lake Kivu? Arguments for a risk assesment in light of the
982 Nyiragongo volcano eruption of 2002. *Acta vulcanologica*, *14*(1-2), 115-122.
983 doi:10.1400/19084

984 Schmidt, W. (1928). Über die Temperatur- und Stabilitätsverhältnisse Von Seen. *Geografiska Annaler*,
985 *10*(1-2), 145-177. doi:10.1080/20014422.1928.11880475

986 Schultze, M., Bohrer, B., Wendt-Potthoff, K., Katsev, S., & Brown, E. T. (2017). Chemical Setting and
987 Biogeochemical Reactions in Meromictic Lakes. In R. D. Gulati, E. S. Zadereev, & A. G.
988 Degermendzhi (Eds.), *Ecology of Meromictic Lakes* (pp. 35-59): Springer.

989 Schwefel, R., Gaudard, A., Wüest, A., & Bouffard, D. (2016). Effects of climate change on deepwater
990 oxygen and winter mixing in a deep lake (Lake Geneva): Comparing observational findings
991 and modeling. *Water Resources Research*, *52*(11), 8811-8826. doi:10.1002/2016WR019194

992 Schwefel, R., Müller, B., Boisgontier, H., & Wüest, A. (2019). Global warming affects nutrient
993 upwelling in deep lakes. *Aquatic Sciences*, *81*(3), 50. doi:10.1007/s00027-019-0637-0

994 Schwefel, R., Steinsberger, T., Bouffard, D., Bryant, L. D., Müller, B., & Wüest, A. (2018). Using small-
995 scale measurements to estimate hypolimnetic oxygen depletion in a deep lake. *Limnology*
996 *and Oceanography*, *63*(S1), S54-S67. doi:10.1002/lno.10723

997 Shatwell, T., Adrian, R., & Kirillin, G. (2016). Planktonic events may cause polymictic-dimictic regime
998 shifts in temperate lakes. *Scientific Reports*, *6*, 24361. doi:10.1038/srep24361

999 Shatwell, T., Thiery, W., & Kirillin, G. (2019). Future projections of temperature and mixing regime of
1000 European temperate lakes. *Hydrology and Earth System Sciences*, 23(3), 1533-1551.
1001 doi:10.5194/hess-23-1533-2019

1002 Shimoda, Y., Azim, M. E., Perhar, G., Ramin, M., Kenney, M. A., Sadraddini, S., . . . Arhonditsis, G. B.
1003 (2011). Our current understanding of lake ecosystem response to climate change: What have
1004 we really learned from the north temperate deep lakes? *Journal of Great Lakes Research*,
1005 37(1), 173-193. doi:10.1016/j.jglr.2010.10.004

1006 Søndergaard, M., Jensen, J. P., & Jeppesen, E. (2003). Role of sediment and internal loading of
1007 phosphorus in shallow lakes. *Hydrobiologia*, 506(1-3), 135-145.
1008 doi:10.1023/B:HYDR.0000008611.12704.dd

1009 Soranno, P. A., Carpenter, S. R., & Lathrop, R. C. (1997). Internal phosphorus loading in Lake
1010 Mendota: response to external loads and weather. *Canadian Journal of Fisheries and Aquatic
1011 Sciences*, 54(8), 1883-1893. doi:10.1139/f97-095

1012 Straile, D., Jöhnk, K., & Henno, R. (2003). Complex effects of winter warming on the physicochemical
1013 characteristics of a deep lake. *Limnology and Oceanography*, 48(4), 1432-1438.
1014 doi:10.4319/lo.2003.48.4.1432

1015 Strogatz, S. H. (1994). *Nonlinear Dynamics and Chaos - With Applications to Physics, Biology,
1016 Chemistry and Engineering*: Addison-Wesley.

1017 Suding, K. N., & Hobbs, R. J. (2009). Threshold models in restoration and conservation: a developing
1018 framework. *Trends in ecology & evolution*, 24(5), 271-279. doi:10.1016/j.tree.2008.11.012

1019 Sugiyama, N., Kravtsov, S., & Roebber, P. (2017). Multiple climate regimes in an idealized lake–ice–
1020 atmosphere model. *Climate Dynamics*, 50(1-2), 655-676. doi:10.1007/s00382-017-3633-x

1021 Tanentzap, A. J., Yan, N. D., Keller, B., Girard, R., Heneberry, J., Gunn, J. M., . . . Taylor, P. A. (2008).
1022 Cooling lakes while the world warms: Effects of forest regrowth and increased dissolved
1023 organic matter on the thermal regime of a temperate, urban lake. *Limnology and
1024 Oceanography*, 53(1), 404-410. doi:10.4319/lo.2008.53.1.0404

1025 Tang, K. W., Flury, S., Grossart, H. P., & McGinnis, D. F. (2017). The Chaoborus pump: Migrating
1026 phantom midge larvae sustain hypolimnetic oxygen deficiency and nutrient internal loading
1027 in lakes. *Water research*, 122, 36-41. doi:10.1016/j.watres.2017.05.058

1028 Tang, K. W., Flury, S., Vachon, D., Ordonez, C., & McGinnis, D. F. (2018). The phantom midge menace:
1029 Migratory Chaoborus larvae maintain poor ecosystem state in eutrophic inland waters.
1030 *Water research*, 139, 30-37. doi:10.1016/j.watres.2018.03.060

1031 Ummenhofer, C. C., & Meehl, G. A. (2017). Extreme weather and climate events with ecological
1032 relevance: a review. *Philosophical Transactions of the Royal Society B*, 372(1723), 20160135.
1033 doi:10.1098/rstb.2016.0135

1034 Vachon, D., Langenegger, T., Donis, D., & McGinnis, D. F. (2019). Influence of water column
1035 stratification and mixing patterns on the fate of methane produced in deep sediments of a
1036 small eutrophic lake. *Limnology and Oceanography*, 64(5), 2114-2128.
1037 doi:10.1002/lno.11172

1038 Vonlanthen, P., Bittner, D., Hudson, A. G., Young, K. A., Muller, R., Lundsgaard-Hansen, B., . . .
1039 Seehausen, O. (2012). Eutrophication causes speciation reversal in whitefish adaptive
1040 radiations. *Nature*, 482(7385), 357-362. doi:10.1038/nature10824

1041 Wetzel, R. G. (2001). *Limnology: Lake and River Ecosystems*: Gulf Professional Publishing.

1042 Wilhelm, S., & Adrian, R. (2008). Impact of summer warming on the thermal characteristics of a
1043 polymictic lake and consequences for oxygen, nutrients and phytoplankton. *Freshwater
1044 Biology*, 53(2), 226-237. doi:10.1111/j.1365-2427.2007.01887.x

1045 Winder, M., & Hunter, D. A. (2008). Temporal organization of phytoplankton communities linked to
1046 physical forcing. *Oecologia*, 156(1), 179-192. doi:10.1007/s00442-008-0964-7

1047 Winder, M., & Sommer, U. (2012). Phytoplankton response to a changing climate. *Hydrobiologia*,
1048 698(1), 5-16. doi:10.1007/s10750-012-1149-2

1049 Woolway, R. I., & Merchant, C. J. (2019). Worldwide alteration of lake mixing regimes in response to
1050 climate change. *Nature Geoscience*, 12(4), 271-276. doi:10.1038/s41561-019-0322-x

1051 Woolway, R. I., Merchant, C. J., Van Den Hoek, J., Azorin-Molina, C., Nöges, P., Laas, A., . . . Jones, I. D.
1052 (2019). Northern Hemisphere Atmospheric Stilling Accelerates Lake Thermal Responses to a
1053 Warming World. *Geophysical Research Letters*, *46*(21), 11983-11992.
1054 doi:10.1029/2019gl082752

1055 Wüest, A., Piepke, G., & Van Senden, D. C. (2000). Turbulent kinetic energy balance as a tool for
1056 estimating vertical diffusivity in wind-forced stratified waters. *Limnology and Oceanography*,
1057 *45*(6), 1388-1400. doi:10.4319/lo.2000.45.6.1388

1058 Yang, Y., Colom, W., Pierson, D., & Pettersson, K. (2016). Water column stability and summer
1059 phytoplankton dynamics in a temperate lake (Lake Erken, Sweden). *Inland Waters*, *6*(4), 499-
1060 508. doi:10.1080/IW-6.4.874

1061 Yankova, Y., Neuenschwander, S., Koster, O., & Posch, T. (2017). Abrupt stop of deep water turnover
1062 with lake warming: Drastic consequences for algal primary producers. *Scientific Reports*, *7*(1),
1063 13770. doi:10.1038/s41598-017-13159-9

1064 Ye, X., Anderson, E. J., Chu, P. Y., Huang, C., & Xue, P. (2018). Impact of Water Mixing and Ice
1065 Formation on the Warming of Lake Superior: A Model-guided Mechanism Study. *Limnology
1066 and Oceanography*, *64*(2), 558-574. doi:10.1002/lno.11059

1067 Zhang, Y., Wu, Z., Liu, M., He, J., Shi, K., Zhou, Y., . . . Liu, X. (2015). Dissolved oxygen stratification and
1068 response to thermal structure and long-term climate change in a large and deep subtropical
1069 reservoir (Lake Qiandaohu, China). *Water research*, *75*, 249-258.
1070 doi:10.1016/j.watres.2015.02.052

1071 Zhong, Y., Notaro, M., Vavrus, S. J., & Foster, M. J. (2016). Recent accelerated warming of the
1072 Laurentian Great Lakes: Physical drivers. *Limnology and Oceanography*, *61*(5), 1762-1786.
1073 doi:10.1002/lno.10331

1074 Zohary, T., & Ostrovsky, I. (2011). Ecological impacts of excessive water level fluctuations in stratified
1075 freshwater lakes. *Inland Waters*, *1*(1), 47-59. doi:10.5268/iw-1.1.406

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1079 **Figure captions**

1080 *Figure 1: Overview of the physical, chemical and biological components and processes in*
1081 *deep lakes considered in the text. Energy fluxes at the air-water interface (P1) represent the*
1082 *interaction between climate and the lake. Thermal stratification (P2) is important for*
1083 *transport between water layers, and is formed primarily by higher water temperatures (P3) in*
1084 *the surface layers compared to bottom layers. Light penetration (P4) causes heating of*
1085 *surface layers and is essential for phytoplankton growth. Deep-water mixing (P5) can occur*
1086 *as a result of strong convective cooling and marks the end of the stratified season. Wind*
1087 *stress (P6) also promotes mixing and deepening of the mixed layer. Ice cover (P7) affects*
1088 *surface heat fluxes and reduces effects of wind on the lake interior. Oxygen concentration*

1089 (B1) is linked to many chemical and biological processes in the water column. Nutrient
1090 concentrations (B2) in the epilimnion are essential for the growth of phytoplankton. Nutrients
1091 and other type of solutes can be released from the sediment (B3). Coloured dissolved organic
1092 matter (CDOM, B4) reduces light penetration in the water column. Greenhouse gases can be
1093 emitted from the sediment (B5). In case the deep-water layers of a lake are heavier than the
1094 overlying water due to solute content, meromixis is formed (B6). Phytoplankton biomass (B7)
1095 grows on nutrients and light in the photic zone of the lake. Some phytoplankton species have
1096 variable buoyancy (B8) that enables uptake of nutrients from below the thermocline.

1097

1098 *Figure 2: a) The associated feedbacks for a shift from a polymictic to a seasonally stratified*
1099 *regime. The effect of climate warming is shown in red. A reference to the corresponding*
1100 *process in Figure 1 is given between brackets. Three feedback loops are formed. Both the*
1101 *purple and the orange feedback loops are positive (i.e. self-reinforcing). The blue, negative*
1102 *feedback loop activates when the turbidity that supports the stratification is caused by sinking*
1103 *particles. b) State diagram of a shift from a polymictic lake of intermediate depth to a*
1104 *seasonally stratified regime. Climate warming increases the duration of stratification events.*
1105 *When these periods become long enough to trigger a reduction in transparency, in some years*
1106 *there might be a sudden jump to a longer stratified period. This will most likely occur in small*
1107 *lakes, where transparency has the strongest control on stratification patterns (blue line). If*
1108 *the turbidity is caused by sinking particles, sedimentation of particles will likely result in*
1109 *clearer water and the breakdown of stratification. In larger lakes, or lakes where the positive*
1110 *feedbacks are only weak, the increase in duration of stratification will be more linear (green*
1111 *line). In a seasonally stratified regime, a reduction in transparency will not, or only*
1112 *marginally, increase the length of the stratified period.*

1113

1114 *Figure 3: a) The associated feedbacks for a shift from a dimictic to a monomictic regime. The*
1115 *effect of climate warming is shown in red. A reference to the corresponding process in Figure*
1116 *1 is given between brackets. Two feedback loops are formed. The blue feedback loop is*
1117 *negative (i.e. self-stabilising), while the orange loop is positive (self-reinforcing). b) State*
1118 *diagram of a shift from a dimictic to a monomictic regime. Inter-annual thermal memory is*
1119 *supported by a large heat storage capacity and the positive feedback in (a). In case of a*
1120 *dominant memory effect, shifts in mixing regime would have a sudden nature (blue line and*
1121 *arrows), while if the memory effect is not dominant (green line), there is a smoother*
1122 *transition, with alternating dimictic and monomictic years. The length of the dotted arrows*
1123 *denotes the probability of a regime shift from one mixing regime to another.*

1124

1125 *Figure 4: a) The associated feedbacks for a shift from a holomictic to an oligo- or meromictic*
1126 *regime. The effect of climate warming is shown in red. A reference to the corresponding*
1127 *process in Figure 1 is given between brackets. The negative (self-stabilising) feedback loop,*
1128 *in blue, causes a decrease in the density of the hypolimnion after incomplete mixing, while the*
1129 *positive (self-reinforcing) feedback loops, in purple and orange, stimulate a density increase.*
1130 *b) State diagram of a shift from a holomictic to either an oligomictic or a meromictic regime.*
1131 *When incomplete mixing occurs as a result of warming, an oligomictic regime is formed. This*
1132 *increases the chances of forming anoxia and solute accumulation, potentially resulting in a*
1133 *meromictic regime if the density increase by solute build-up (positive feedbacks) exceeds the*
1134 *density decrease by hypolimnetic warming (negative feedback). The length of the dotted*
1135 *arrows denotes the probability of a regime shift from an oligomictic to a meromictic regime,*
1136 *but the possibility for this shift depends on lake-specific characteristics. A shift is most likely*
1137 *to occur in lakes with little deep-water renewal, where large quantities of solutes can be*
1138 *released from the sediment.*