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REVIEW

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

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Abstract

1. Climate warming is causing changes in the physics of deep lakes, such as longer summer stratification, increased water column stability, reduced ice cover, and a shallower depth of winter overturns. An ultimate consequence of warming would be a transition to a different mixing regime. Here we investigate the role of physical, chemical, and biological feedback mechanisms that unfold during a shift in mixing regime, and whether these feedbacks could prompt and stabilise the new regime. Although climate, interannual temperature variation, and lake morphometry are the main determinants of a mixing regime, when climate change causes shifts in mixing regime, internal feedback mechanisms may gain in importance and modify lake ecosystem functioning.
2. We review the role of these feedbacks in three mixing regime shifts: from polymictic to seasonally stratified, from dimictic to monomictic, and from holomictic to oligomictic or meromictic.
3. Polymictic lakes of intermediate depth (*c.* 3–10 m mean depth) could experience seasonal stratification if a stratification event triggers phytoplankton blooms or dissolved organic matter release, reducing transparency and therefore further heating the surface layer. However, this feedback is only likely to have influence in small and clear lakes, it would be easily disturbed by weather conditions, and the resulting stratified state does not remain stable in the long term, as stratification is lost in winter.
4. The ice-albedo feedback might cause an accelerated shift from ice-covered (dimictic) to ice-free (monomictic) winters in sufficiently deep (mean depth 50 m or more) lakes, where temperature memory is carried over from one winter to the next. Nevertheless, there is an ongoing debate into whether this process can persist during natural weather variations and overcome self-stabilising mechanisms such as thermal insulation by snow. The majority of studies suggest that a gradual transition from dimictic to monomictic is more likely than an abrupt transition.
5. A shift from a holomictic to a meromictic regime can occur if anoxia is triggered by incomplete mixing and an increase in deep-water density—through the

accumulation of solutes—exceeds a density decrease by hypolimnetic warming. A shift to meromixis would strongly alter the biology of a lake and might be difficult to reverse. If solutes accumulate only minimally in the hypolimnion, an oligomictic regime is formed, in which years with complete and incomplete mixing alternate.

6. Understanding the importance of feedback mechanisms and the role of biogeochemistry when lakes shift in mixing regime could lead to a better understanding of how climate change affects lake ecosystems.

KEYWORDS

climate change, meromixis, mixing regime, stratification, water transparency

1 | INTRODUCTION

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

In the present review paper, we look at the physical, chemical, and biological consequences of climate warming and increased density stratification in deep lakes, defined here as lakes that stratify during at least one season. We then identify internal feedbacks that can reinforce (positive feedbacks) or slow down (negative feedbacks) shifts between mixing regimes. The scope of this paper only includes regime shifts where such feedback loops were identified in the existing literature, or where they could be constructed using individual processes, and considers mixing regime shifts in the context of increasing atmospheric temperatures. The potential importance of feedbacks is well illustrated by the alternative macrophyte- (clear-water) and algae-dominated (turbid) states in shallow lakes (Ibelings et al., 2007). Regime shifts between these two states involve feedback loops between turbidity, nutrients, and trophic interactions that retain either state, also in the face of changing external processes such as eu-/oligotrophication or perturbations such as storms (Scheffer, 1998; Scheffer et al., 2001).

In deep, stratified lakes the vertical distribution of oxygen, nutrients, and phytoplankton are strongly influenced by density stratification, which hints at the potential of mixing regimes to act as important drivers of ecosystem functioning. Mixing regimes are primarily driven by physical processes, and therefore under direct influence of climate change (Livingstone, 2008; for definitions of mixing regimes, see Box 1). Mixing regimes in deep lakes differ from one another in several physical, chemical, and biological aspects (Adrian et al., 2009; Boehrer & Schultze, 2008; North et al., 2014). According to the classical view on mixing regimes (Hutchinson & Löffler, 1956; Lewis, 1983), local climate and morphometry are the main factors determining the mixing regime of a lake. However, factors other than depth and climate, such as transparency (Brothers et al., 2014) and solute content (Boehrer & Schultze, 2008), can also influence lake mixing. Conversely, mixing regimes might influence these factors. Thus, lake-internal feedbacks could stabilise and even determine the mixing regime, especially in situations where morphometry and climate can support multiple mixing regimes. It is in these situations that mixing regime shifts are to be expected, and already unfolding, in response to ongoing climate change. If self-sustaining feedback mechanisms hold the new regime in place, shifts in mixing regime may prove to be resilient.

Quantitative observations and numerical simulations specifically focusing on shifts in mixing regime by factors other than temperature are scarce, as long-term observations and detailed studies are needed to observe such shifts and identify the drivers. However, individual processes that could lead to feedback loops stabilising mixing regimes, are well described. In what follows, we review the literature on the physical trends related to increased duration and strength of density stratification, and the chemical and biological consequences thereof (Figure 1). Following this literature review, we derive processes at play during a transition in mixing regime and discuss their interaction in typical lake regime shifts. The observed feedbacks are brought together, visualised, and placed into the perspective of shifts in mixing regime under increasing temperatures. We also discuss the limitations of the relevance of each feedback and specify for what types of lakes these feedbacks may be considered. In this way, we believe our review provides new and pertinent information on how climate warming

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 local climate, depth, salinity, and lake morphology, a lake mixes a certain number of times per year (never—amictic, once—monomictic, twice—dimictic, three or more times—polymictic), either completely—always from top to bottom (holomixis)—only sometimes from top to bottom (oligomixis) or always partially (meromixis). Shallow lakes tend to be *polymictic*, i.e. they mix multiple times per year, although 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 3–20 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, i.e. over at least a season, density stratification is used here 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 low 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 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 5 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). We reserve the term *meromictic* 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).

may affect lake ecosystems, extending beyond direct effects of temperature alone.

2 | PHYSICAL, CHEMICAL, AND BIOLOGICAL CONSEQUENCES OF ENHANCED STRATIFICATION

2.1 | Water temperatures and stratification

(Figure 1: P1, P2, P3) The increase in global surface air temperature (IPCC, 2014) has an impact on lake temperature and water column stratification. Global surveys of surface water temperatures report an increase in epilimnetic temperatures with rates roughly between 0.2 and 1°C per decade (Kraemer et al., 2015; O'Reilly et al., 2015; Shimoda et al., 2011). The temperature difference between epi- and hypolimnion often increases, causing longer and stronger thermal stratification in summer (Fang & Stefan, 1999; Foley et al., 2012; Kraemer et al., 2015). Even when temperature differences remain the same, the density difference becomes greater with warming, as the water density-temperature relation is steeper at higher temperatures (Wetzel, 2001). As the density difference between epi- and hypolimnion increases, mixing of the two layers is reduced, which further heats the surface layer and increases density differences, as less heat is transported downwards. The stability of the water column is often expressed as the Schmidt stability (i.e. the potential energy stored in stratification per unit area; Idso, 1973; Schmidt, 1928). Between 1970 and 2010, average Schmidt stability in lakes worldwide has increased by up to 25% (Kraemer et al., 2015).

(Figure 1: P2) A larger density difference between the epilimnion and hypolimnion increases the local stability of the water column. An increase in stability reduces the vertical turbulent diffusivity

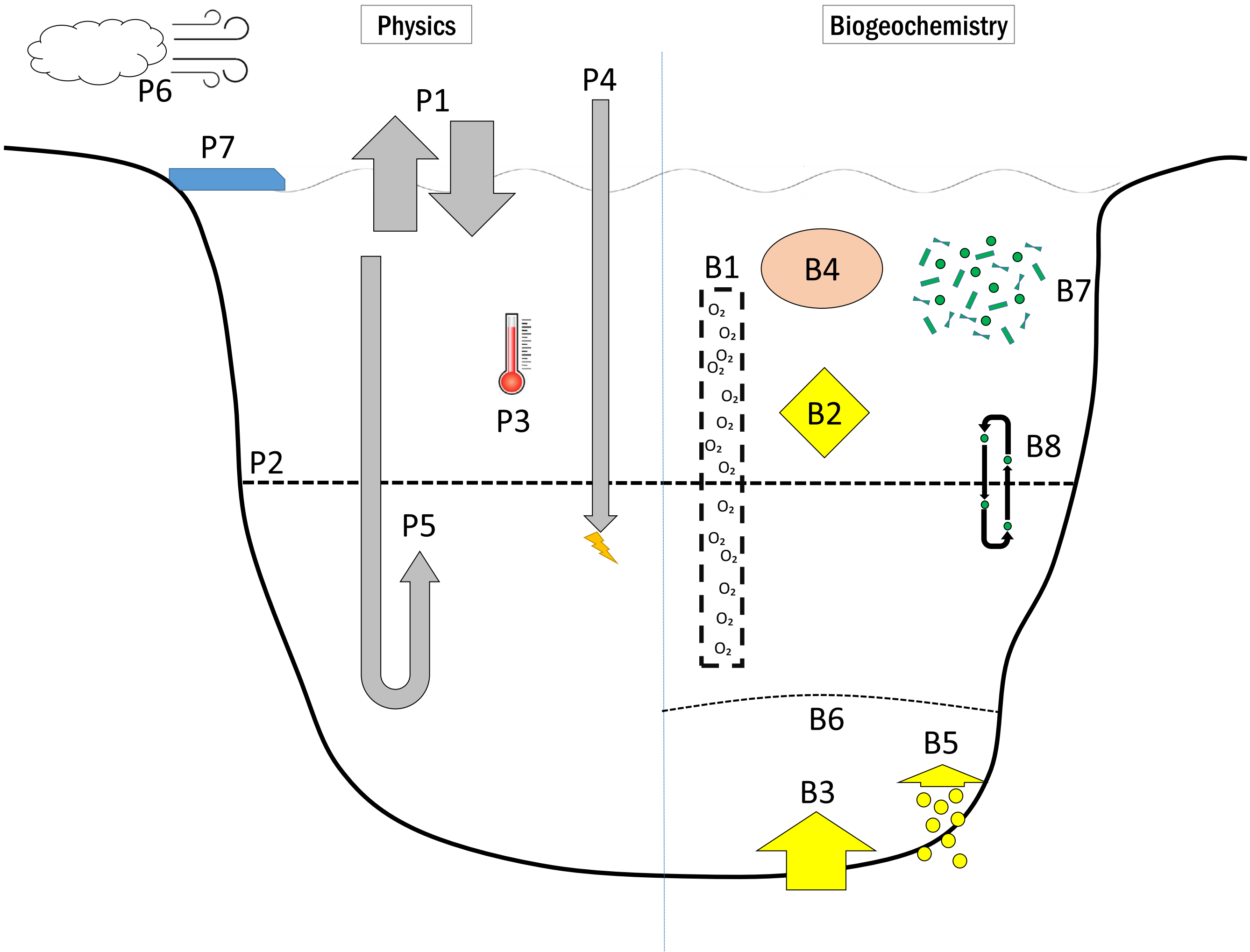

FIGURE 1 Overview of the physical and biogeochemical components and processes in deep lakes considered in the text. P denotes a physical and B a biogeochemical process. Energy fluxes at the air–water interface (P1) represent the interaction between climate and the lake. Thermal stratification (P2) is important for transport between water layers and is formed primarily by higher water temperatures (P3) in the surface layers compared to bottom layers. Light penetration (P4) causes heating of surface layers and is essential for phytoplankton growth. Deep-water mixing (P5) can occur as a result of strong convective cooling and marks the end of the stratified season. Wind stress (P6) also promotes mixing and deepening of the mixed layer. Ice cover (P7) affects surface heat fluxes and reduces effects of wind on the lake interior. Oxygen concentration (B1) is linked to many chemical and biological processes in the water column. Nutrient concentrations (B2) in the epilimnion are essential for the growth of phytoplankton. Nutrients and other type of solutes can be released from the sediment (B3). Coloured dissolved organic matter (CDOM, B4) reduces light penetration in the water column. Greenhouse gases can be emitted from the sediment (B5). If the deep-water layers of a lake are heavier than the overlying water due to solute content, meromixis is formed (B6). Phytoplankton biomass (B7) grows through consumption of resources such as like nutrients and light in the photic zone of the lake. Some cyanobacteria have variable buoyancy (B8) that enables uptake of nutrients from below the thermocline, or they may use their buoyancy to form deep chlorophyll maxima in the metalimnion of the lake

K_z, which indicates the rate of vertical mixing (Ravens et al., 2000; Wüest et al., 2000). Hence, a stronger stratification implies that dissolved substances less easily traverse the thermocline, promoting separation between surface and bottom waters.

2.2 | Oxygen dynamics in deep lakes

(Figure 1: P2, P4, P5, B1) Oxygen sources (reaeration and photosynthesis) are mainly restricted to the epi- and metalimnion (Giling, Staehr, et al., 2017; Obrador et al., 2014; Wetzel, 2001), and in most lakes oxygen is constantly being depleted in the hypolimnion, especially near the sediment. Generally, deep convective mixing is the major source of oxygen replenishment in the deep-water layers (Straile et al., 2003), although river intrusion can also notably affect hypolimnetic oxygen conditions (Fink et al., 2016). The extent of the oxygen-depleting processes in the water column and the sediment, the volume of the hypolimnion, and the sediment area to hypolimnion volume ratio define the rate at which oxygen concentrations fall after installation of the thermocline (Schwefel et al., 2018). Hypolimnia of highly productive systems have a higher oxygen depletion rate (Müller et al., 2012; Rippey & McSorley, 2009). Deeper lakes contain more oxygen due to a thicker hypolimnion, and oxygen depletion rates tend to decrease with depth, so deeper lakes are less prone to become anoxic in one summer (Müller et al., 2012; Schwefel et al., 2018). However, they are less likely to experience complete vertical mixing, and climate warming further decreases this likelihood. In the case of incomplete mixing, the oxygen is only partially replenished and the hypolimnion will experience lower oxygen levels the following year. Therefore, a shift from holomictic to oligomictic behaviour implies a greater risk of anoxic conditions, for productive lakes in particular.

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

2.3 | Influence of anoxia on nutrient distribution and other substances

(Figure 1: B1, B2, B3) Anoxia near the sediment can induce enhanced internal phosphorus loading through reduction of the benthic redox potential, so that iron-bound phosphate is released from the sediment (Søndergaard et al., 2003). While this enhanced release can be relevant on short time scales, on seasonal (or longer) time scales internal P budgets are mostly dependent on settling and mineralisation rates, as well as sediment characteristics (Hupfer & Lewandowski, 2008). During stratification, P tends to accumulate in the hypolimnion as nutrients are not mixed into the photic zone while mineralisation in the sediment and pelagic continues. When deep mixing occurs, large amounts of P can enter the photic zone, potentially boosting productivity (Lehmann et al., 2015; Lepori et al., 2018). Nitrogen can also be released from the sediment under anoxic conditions in the form of ammonium (Wetzel, 2001). Denitrification occurs in anoxic hypolimnia and, especially, sediments (Wetzel, 2001). It is a major loss term of nitrogen in lakes. When anoxia of the hypolimnion is ended by a mixing event, nitrogen, like phosphorus, can enter the photic zone and boost productivity. However, large losses of nitrogen to the atmosphere can occur through denitrification, as nitrate-rich water is brought in contact with the anoxic sediment (De Brabandere et al., 2015; Lehmann et al., 2015).

(Figure 1: P5, P6, B1, B2, B3) The stratification that is at the root of build-up of nutrients in the hypolimnion, however, also prevents nutrients from entering the epilimnion, as increased stratification implies that dissolved substances are retained more in their respective layers. Reduced entrainment of deeper water layers and less intense winter mixing could cause decreased nutrient concentrations in the epilimnion, despite the higher nutrient concentrations in the hypolimnion (Schwefel et al., 2019; Yankova et al., 2017). As nutrients accumulate in the hypolimnion because of increased stratification with climate change, the amount of nutrients released to the epilimnion when complete mixing does occur goes up.

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

2.4 | Influence of mixing dynamics on lake phytoplankton

(Figure 1: B2, B7) A change in nutrients in the epilimnion will strongly control phytoplankton development. As mentioned above, increased stratification might actually reduce nutrient levels in the surface water of lakes. Longer stratification in such a case means a longer period of nutrient limitation for phytoplankton (Yang et al., 2016) and therefore a bigger advantage for species that efficiently use or store nutrients (Winder & Sommer, 2012), and potentially for mixotrophic species, which have access to additional organic nutrient sources (Jansson et al., 1996). However, the effects of increased stratification and warming of surface waters differ between oligotrophic and eutrophic systems. In oligotrophic systems, a higher metabolic rate driven by higher temperatures in combination with nutrient shortage can lead to lower levels of biomass compared to colder temperatures, while in eutrophic systems, the higher temperature may boost growth and biomass (Jöhnk et al., 2008; Kraemer et al., 2017).

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

(Figure 1: P5, B2, B7, B8) Higher nutrient concentrations in the hypolimnion do not directly promote phytoplankton growth because of the lack of light at depth, with the exception of phytoplankton species that produce a deep chlorophyll maximum in the metalimnion (e.g. *Planktothrix rubescens*), or buoyancy regulators that are perceived to make excursions into the hypolimnion (e.g. *Microcystis*; Fee, 1976; Paerl & Huisman, 2009). The strong vertical heterogeneity in nutrient levels induces the possibility that mixing events causing entrainment of hypolimnetic water into the epilimnion can lead to spikes of epilimnetic nutrient concentrations (Lehmann et al., 2015), stimulating phytoplankton blooms (Giling, Nejstgaard, et al., 2017). These events can be caused by extreme weather events such as storms, cold spells, or river floods (Crockford et al., 2015; Soranno et al., 1997). With increased stratification in summer, the amount of energy needed for these deep mixing events increases, but the nutrient pulse after such an event tends to be stronger (Coats et al., 2006).

3 | SHIFTS IN MIXING REGIME

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

Two other shifts in mixing regime can also be expected with climate change, mediated through changes in hydrology. In lakes where water level is projected to decrease with climate change, a shift from stratified to polymictic can be expected if the water level falls below a critical value to sustain seasonal stratification (Kirillin & Shatwell, 2016; Zohary & Ostrovsky, 2011). Increase in water level could cause a shift in the opposite direction. Both temperature and water level can be a driver of a shift between polymictic and stratified regimes, and the feedbacks we discuss in the following section apply to both. In saline lakes, a reduction of freshwater inflow can cause a shift from meromictic to holomictic, as the freshwater layer on top of the heavier saline layer diminishes (Gertman & Hecht, 2002; Kaden et al., 2010) and vice versa with an increase in precipitation (Melack & Jellison, 1998). We are not aware of literature that describes feedbacks from the new mixing regime to the hydrological input, or changed biogeochemical conditions under the new regime that affect the vertical salt distribution in a way that affects the new regime's stability. Our view is therefore that such a response of the saline lake mixing regime is a direct function of the discharge and seasonality of the external inflow (although a threshold response is possible), and because of the lack of known internal feedbacks, we will not treat this regime shift further.

3.1 | Shift from a polymictic to a seasonally stratified regime

Lakes of intermediate depth (*c*. 3–10 m mean depth, Kirillin & Shatwell, 2016) can support both polymictic and seasonally stratified (dimictic or monomictic) regimes, based on morphometry, transparency, wind speed, and annual mean solar radiation flux (Kirillin & Shatwell, 2016). A shift from polymixis to seasonal stratification might occur as a result of climate warming in these lakes (Kirillin, 2010; Woolway & Merchant, 2019). This trend can be amplified by reduced water transparency and lower wind speeds in summer (Shatwell et al., 2016). If transparency is reduced, less energy penetrates to deeper layers, as more solar radiation is absorbed near the surface. This can result in warming of the surface layer, cooling of the hypolimnion, and overall stronger stratification (Jones et al., 2005; Tanentzap et al., 2008), but the influence of transparency on stratification is significantly stronger in smaller lakes due to a lower contribution of wind mixing to turbulence formation (Fee et al., 1996). A decrease in transparency can be caused by phytoplankton growth or increased CDOM content, for example as a consequence of catchment-based inflow of nutrients or organic matter. CDOM loading from peatlands or forests may increase as a function of climate change, for example through increased decomposition rates at higher temperatures (Jennings et al., 2010). Wind is a crucial factor in exchanging heat between atmosphere and lakes by inducing mixing (Imboden & Wüest, 1995), and can be a decisive factor for hypolimnetic temperature trends. Indeed, decreasing wind speeds cause a cooling of the hypolimnion by reducing heat transfer to deep-water layers (Magee & Wu, 2017). Regional trends in wind speed might have the potential to cause a shift in mixing regimes (Woolway et al., 2019). However, wind forcing is external to the lake system, and we are not aware of literature describing feedbacks between wind forcing and lake conditions that reinforce either the polymictic or stratified mixing regime.

Periods with warm and calm weather are promoted by climate change, and can induce stratification events in polymictic lakes, lasting multiple days or even weeks (Wilhelm & Adrian, 2008). However, strong inter-annual variation in the duration of stratification within the same lake has been documented that cannot be explained by temperature changes alone (Brothers et al., 2014; Riis

& Sand-Jensen, 1998). Water transparency was determined to be a major factor of shifts in mixing regime in the studies of Riis and Sand-Jensen (1998), Brothers et al. (2014), and Shatwell et al. (2016), and is, as stated, influenced by phytoplankton growth and CDOM content.

In this paper, we are interested in feedbacks that would stabilise a newly established stratified regime, such as mechanisms that would perpetuate lower transparency. Brothers et al. (2014) described such a feedback in a eutrophic German lake with an average depth of 1.7 m (maximum 2.9 m) and a surface area of 3.3 ha. Strong rainfall flooded surrounding peatlands, leading to increased CDOM and nutrient concentrations and higher water levels (about 1 m) in the lake. Transparency was reduced due to a combination of increased CDOM and phytoplankton, which caused stratification and anoxia near the sediment, and promoted internal loading of CDOM and nutrients from the sediment, stabilising the stratified state. For a different lake, Riis and Sand-Jensen (1998) describe almost a doubling of the duration of stratification over a period of 40 years due to increased CDOM concentrations in an oligotrophic Danish lake of 8.1 m mean depth (maximum 12 m) and a surface area of 12 ha, but no stabilising feedbacks were identified. Model simulations of two eutrophic German lakes (maximum depths 8 and 9.5 m) by Shatwell et al. (2016) suggested that phytoplankton can have a decisive influence on mixing regimes in lakes of intermediate depth. The presence or absence of a clear-water phase in spring could change the mixing regime for that year. Again, no feedbacks are described. Still, in shallow lakes a heatwave or period of calm can trigger a period of stratification and potentially cause anoxia when oxygen depletion is sufficiently high, followed by nutrient release to the photic zone when stratification ends (Wilhelm & Adrian, 2008). When the accumulated nutrients become available to phytoplankton during stratification, for example due to buoyancy regulation, the ensuing bloom could reduce transparency, leading to stronger heating of the upper water layers (Jones et al., 2005), and thus stabilise the stratified regime.

However, despite the crucial role of transparency in regulating thermal stratification and the study of Brothers et al. (2014) showing the potential of the transparency-reduction feedback in environmental data, this feedback might only apply to a select set of lakes. Below, we give three arguments why the likelihood that this feedback will cause bi-stability of polymixis and seasonal stratification might be limited: (1) the feedback can regularly be overridden by external perturbations unless a specific set of lake conditions, regarding morphometry and transparency, is present; (2) stratification hinders exchange between sediment and surface water, effectively weakening the feedback; and (3) there is a reset of lake conditions in winter and no carry-on of the feedback to the next year.

Lakes that are too shallow cannot sustain seasonal stratification as commonly recurring convective or wind mixing events break down stratification completely. Conversely, deeper lakes often already have a stratified regime, thus restricting bi-stability to lakes with an intermediate depth range (*c.* 3–10 m, Kirillin & Shatwell, 2016). In lakes larger than approximately 5 km^2, wind and convective mixing are the decisive factors to determine the depth of stratification and transparency only has a minor effect (Fee et al., 1996), whereas Kirillin and Shatwell (2016) report a decreasing effect of transparency on mixing regime above a lake length of about 1–10 km based on an analysis of 379 lakes. Therefore, the feedback described above would only be relevant in small lakes of intermediate depth. Additionally, Persson and Jones (2008) show that in already turbid water, a change in transparency has little effect on thermal stability, which would suggest that the transparency-reduction feedback requires an initially low turbidity. If all light was already absorbed in the mixed layer before the reduction of transparency unfolds, a further drop in transparency would not make a large difference in heat distribution (Persson & Jones, 2008). Along the same lines, a sensitivity analysis in the modelling study by Shatwell et al. (2019) indicated that the effect of varying transparency on stratification is strongest in small lakes with low to medium (up to *c.* 1.0 m^{-1}) extinction coefficients.

Stratification restricts exchange of dissolved materials between deep and shallow water layers. Therefore, sediment release of CDOM and nutrients would only marginally reach the epilimnion and affect light penetration. Nutrients would reach the surface layer after a mixing event, as is supported by findings of blooms after the end of stratification events (Wilhelm & Adrian, 2008), but this would break the transparency-reduction feedback. Buoyant cyanobacteria could—potentially—use the nutrients in the hypolimnion and move across the thermocline into the light to grow (Paerl & Huisman, 2009), keeping the feedback loop intact, although the reality of this remains under discussion (Bormans et al., 1999). In the study of Brothers et al. (2014), sediment release of substances did influence the pelagic despite consistent stratification, but the role of the thermocline was not discussed. The presence of a thermocline limits turbulence reaching the sediment, so stratification reduces resuspension of particles that sink to the bottom and promotes sedimentation losses. Formation of stratification can thus reduce particle-based turbidity. The reduced turbidity in turn decreases stratification, completing a negative feedback loop (Figure 2a). If the turbidity is caused by sinking particles (e.g. non-buoyant phytoplankton cells), this negative feedback inhibits sustenance of the stratified state.

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

Summarising, in a polymictic lake of intermediate depth, a seasonally stratified regime can establish under lower wind

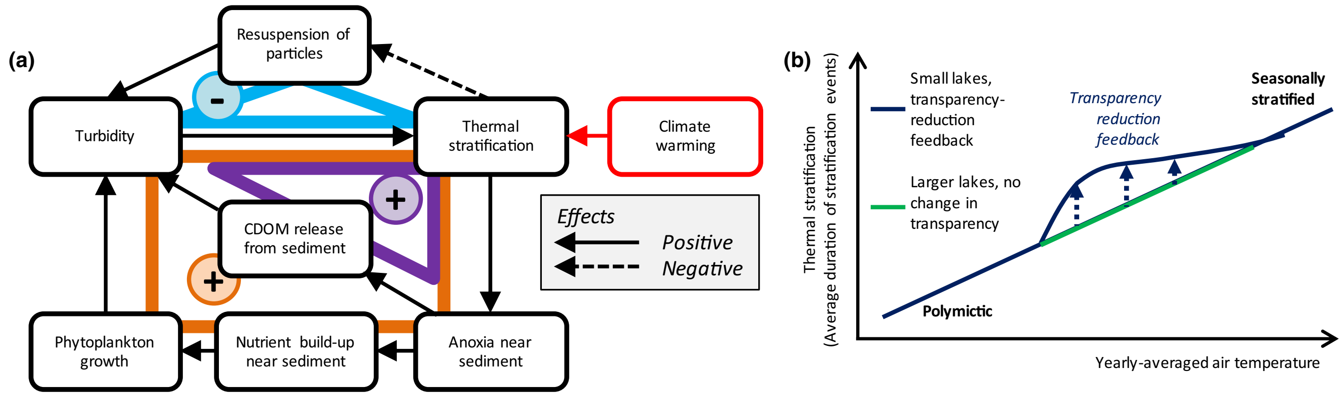

FIGURE 2 (a) The associated feedbacks for a shift from a polymictic to a seasonally stratified regime. Solid arrows denote a stimulating (positive) effect and dashed arrows a reducing (negative) effect. The effect of climate warming is shown in red. Three feedback loops are potentially formed. Both the purple and the orange feedback loops are positive (i.e. self-reinforcing). The blue, negative feedback loop is activated when the turbidity that supports the stratification is reduced because of sinking particles. (b) State diagram of a shift from a polymictic lake of intermediate depth to a seasonally stratified regime. Climate warming increases the duration of stratification events. When these periods become long enough to trigger a reduction in transparency, in some years there might be a sudden jump to a longer stratified period. This is most likely to occur in small lakes, where transparency has the strongest control on stratification patterns (blue line). If the turbidity is caused by sinking particles, sedimentation of these particles will result in clearer water and the breakdown of stratification. In larger lakes, or lakes where the positive feedbacks are only weak, the increase in duration of stratification will be more linear (green line). In a seasonally stratified regime, a reduction in transparency will not, or only marginally, increase the length of the stratified period

speeds, decreased transparency, or a higher water level (Kirillin & Shatwell, 2016). Changes in transparency can strongly influence thermal stability (Persson & Jones, 2008; Tanentzap et al., 2008), and even shift mixing regimes (Brothers et al., 2014; Shatwell et al., 2016). Feedback loops could sustain the stratified state (Figure 2a), which might cause a sudden shift from a polymictic to a seasonally stratified regime for a particular year (Figure 2b). However, as discussed above, there is a suite of reasons why these feedbacks may not be dominant in most lakes.

3.2 | Shift from a dimictic to a monomictic regime

Near the poles, loss of ice cover in deep lakes is likely to turn amictic lakes into cold monomictic lakes, and cold monomictic into dimictic lakes (Nõges et al., 2009). In temperate regions, it forces the two separate mixing events at the end of autumn and the end of spring into one period with a more-or-less uniform temperature profile; a shift from dimixis to monomixis (Ficker et al., 2017; Sharma et al., 2019).

For a freshwater lake of a given morphometry, weather conditions and water temperature determine whether ice forms or not (Leppäranta, 2015). Climate change drives the atmosphere towards warmer conditions, but due to natural variation in weather, perpetuation of ice-free conditions after one ice-free winter is unlikely unless water temperatures express a memory of previous winters. Such a memory might be established due to the large thermal heat capacity of deep lakes and a dominant effect of ice-albedo. Ice has a higher albedo than water (i.e. ice reflects more shortwave radiation), reducing heating of an ice-covered lake. When ice disappears, the surface water warms faster through absorption of solar radiation (Austin & Colman, 2007). A modelling study on the Laurentian Great Lakes under a prescribed weather cycle, atmospheric noise, and slow climatic forcing, showed that ice in deep lakes can prevent lake warming by its high albedo and promotes ice cover in following years (Sugiyama et al., 2017), which we define as a memory effect. Once ice disappeared, deep water layers warmed up to a larger degree, making it harder for water temperature to reach freezing levels in following years.

Only sufficiently deep lakes have the necessary thermal heat capacity to transfer the effect of ice cover to the next winter; Sugiyama et al. (2017) investigated lakes with an average depth of at least 50 m, but do not give a minimum depth required to generate a memory effect. Bi-stability occurred in ranges of annual mean air temperatures of *c*. 0.5°C (for lakes of 50 m depth) and *c*. 1.5°C (for lakes of 150 m depth). Outside of these ranges, the lakes were always ice-covered or always ice-free, regardless of the ice cover in previous winter.

Apart from its higher albedo, ice insulates the lake from the atmosphere, limiting heat loss to the atmosphere in winter (Leppäranta, 2015; Zhong et al., 2016). This insulation works in an opposite direction as the ice-albedo feedback (Figure 3a), and it weakens the memory effect. The relative importance of both processes is still disputed, but Sugiyama et al. (2017) find a dominant ice-albedo feedback with a one- to three-column model. In contrast, at a higher spatial resolution, Zhong et al. (2016) and Ye et al. (2018) did not find a dominant memory effect and state that the role of ice albedo is small, suggesting a smoother transition from dimictic to monomictic with a warming climate. All three modelling studies were performed in a similar environment (the Great Lakes region)

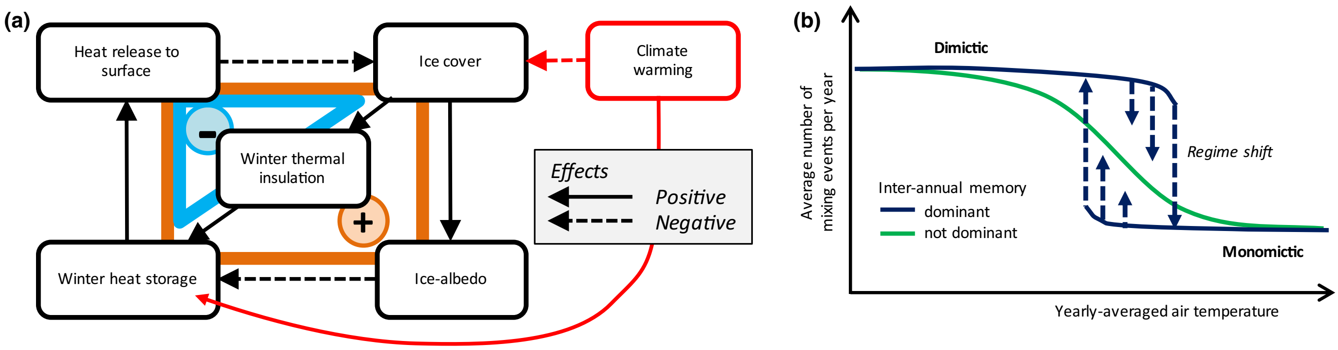

FIGURE 3 (a) The associated feedbacks for a shift from a dimictic to a monomictic regime. Solid arrows denote a stimulating (positive) effect and dashed arrows a reducing (negative) effect. The effect of climate warming is shown in red. Two feedback loops are formed. The blue feedback loop is negative (i.e. self-stabilising), while the orange loop is positive (self-reinforcing). (b) State diagram of a shift from a dimictic to a monomictic regime. Inter-annual thermal memory is supported by a large heat storage capacity and the positive feedback in (a). In case of a dominant memory effect, shifts in mixing regime would have a sudden nature (blue line and arrows), while if the memory effect is not dominant (green line), there is a smoother transition, with alternating dimictic and monomictic years. The length of the dotted arrows denotes the probability of a regime shift from one mixing regime to another

and actively investigated the role of ice-albedo in determining thermal structure. Similar to Zhong et al. (2016) and Ye et al. (2018), the modelling study of Shatwell et al. (2019) reported a gradual shift from ice-covered to ice-free winters in two lakes of 20–30 m mean depth in Europe, rather than an abrupt shift. Other studies on the ice-albedo feedback and thermal memory in lakes are scarce. However, this topic has been addressed for sea ice; modelling studies suggest that the response of sea ice to atmospheric temperature changes might show lags, but is not truly bi-stable (Li et al., 2013; Ridley et al., 2012), and therefore a gradual loss of ice cover is to be expected.

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

3.3 | Shift from a holomictic to an oligo- or meromictic regime

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

However, in oligomictic lakes, there is an interplay between the increase in hypolimnetic temperature and the frequency of complete mixing events. The hypolimnion slowly heats over the year as a result of the geothermal heat flux and as warmer water from the epilimnion is gradually mixed into the deeper layers by turbulence. Incomplete winter mixing fails to cool the hypolimnion, resulting in a warming trend. This increase in hypolimnetic temperature facilitates complete mixing in subsequent years, as less cooling is required for an overturn. Additionally, the higher thermal expansivity of water at higher temperatures can increase the likelihood of complete mixing in lakes with elevated salt concentrations in the hypolimnion (Matzinger et al., 2006). When deep mixing finally occurs during a colder winter, hypolimnetic temperatures show a sudden drop and the resistance to full mixing in subsequent years would increase again. This is why this process is referred to as a *sawtooth pattern* (Livingstone, 1993, 1997). This pattern has been observed in several deep lakes (Coats et al., 2006; Lepori & Roberts, 2015; Straile et al., 2003), and might facilitate sporadic overturn events even under milder temperatures. Climate warming is predicted to lengthen the warming periods and reduce the frequency of turnovers and subsequent cooling (Livingstone, 1997). In accordance with the sawtooth-pattern feedback, a decrease in the extent of winter mixing is expected during ongoing climate warming. However, if a new plateau in air temperatures is reached, the frequency of complete mixing is likely to return to its previous level as hypolimnetic temperatures catch up with winter temperatures, unless meromixis develops.

In both oligomictic and meromictic lakes, oxygen replenishment in the hypolimnion is strongly reliant on sporadically occurring winter mixing, and a reduced frequency of overturns means an increased likelihood of anoxia (Foley et al., 2012; Schwefel et al., 2016). As a secondary effect of the increased anoxia, internal nutrient loading and harmful effects for lake productivity and fish can be expected as a lake shifts from a holomictic to an oligomictic regime (O'Reilly et al., 2003). Internal loading in stratifying lakes changes the distribution of nutrients in the system, by increasing the concentration in the hypolimnion, but affecting the epilimnion only to a lesser extent. As eutrophication also increases oxygen depletion in the hypolimnion, eutrophication and climate warming both increase the risk of anoxia.

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

Endogenic meromixis is a form of meromixis that is sustained by decomposition and increased concentrations of dissolved substances by biogeochemical cycles in the deep water layer (for full explanation, see Boehrer & Schultze, 2008). This leads to the hypothesis of anoxia as a potential trigger for endogenic meromixis (Hutchinson, 1957; Julià et al., 1998). In this situation, the onset of anoxia sets off the formation of a heavier water layer by an increased build-up of solutes in the hypolimnion and complete mixing becomes too infrequent to distribute these solutes through the water column. This build-up of solutes suppresses further mixing and could cause a more abrupt and permanent formation of meromixis. In Lake Lugano (Italy/Switzerland), a large (49 km^2) and deep (maximum depth 288 m) peri-alpine lake, endogenic meromixis might have formed as a result of anthropogenic eutrophication (Lepori et al., 2018). The possibility of meromixis caused by climate change has not been addressed often in scientific literature. Julià et al. (1998) mentioned climate-induced anoxia as a potential cause of meromixis in the Spanish Lake La Cruz, a lake located in a calcite-rich area with a maximum depth of about 23 m. In a modelling study of the oligotrophic, monomictic Lake Ohrid (North Macedonia/Albania, maximum depth 289 m), Matzinger et al. (2007) found that above an atmospheric warming rate of 0.02°C/year, hypolimnetic temperature increase would fall behind surface water warming rates. Additionally, solute accumulation in the hypolimnion would further increase the density of deep waters, preventing complete overturns in future scenarios (Matzinger et al., 2007). The increase in solute concentration must be strong enough to offset a reduction of density by hypolimnetic warming (Figure 4a).

Several physical lake processes can mix surface water into the hypolimnion, even when a chemical gradient is present, therefore reducing density differences. Wind-induced internal waves increase turbulence around the thermocline, and therefore mixing between both layers

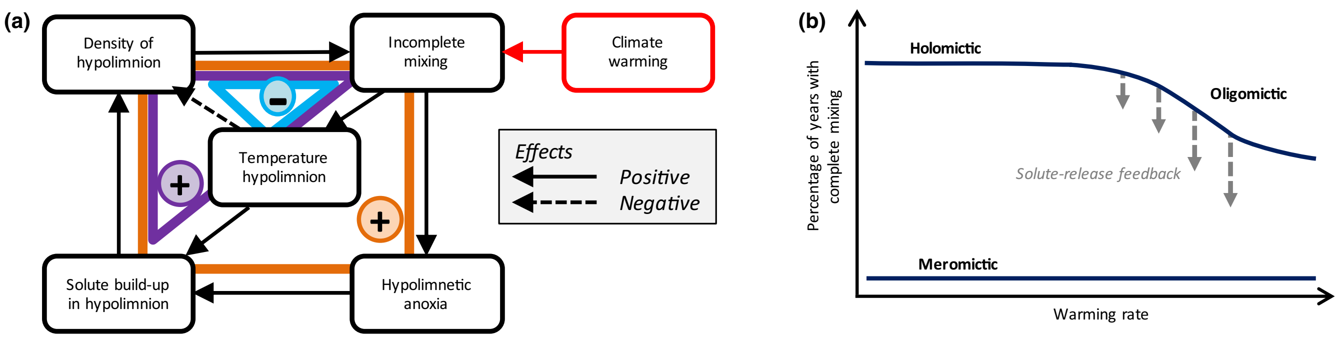

FIGURE 4 (a) The associated feedbacks for a shift from a holomictic to an oligo- or meromictic regime. Solid arrows denote a stimulating (positive) effect and dashed arrows a reducing (negative) effect. The effect of climate warming is shown in red. The negative (self-stabilising) feedback loop, in blue, 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

(Imboden & Wüest, 1995). Differential cooling is the process where shallow areas experience fast convective cooling and this water mass moves downwards along the lake slopes in cases where morphology is suitable. This can lead to transport of water from the surface to deep water layers (Ambrosetti et al., 2010; Peeters et al., 2003). Intrusion of river inflow is another potentially important factor for deep-water renewal (Ambrosetti et al., 2010). Depth of river intrusion depends on inflow water temperature and lake thermal structure, amongst others (Fink et al., 2016). High sediment densities in the inflow can increase water density and allow penetration into the hypolimnion (Fink et al., 2016; Loizeau & Dominik, 2000). In lakes where these processes cause significant deep-water renewal, a shift to meromixis is less probable. Formation of meromixis due to climate warming is also not likely in dimictic or polymictic lakes where complete mixing is frequent, but could occur in monomictic lakes in multiple climate zones.

It is difficult to determine in which lakes a shift towards meromixis is most likely to occur. Prime candidates are lakes that did not experience prolonged periods of anoxia and incomplete mixing until now, but are susceptible with the effects of climate change. Deeper lakes in particular seem to be vulnerable due to their tendency to mix incompletely (Danis et al., 2004). H these are not the only factors, as the chemical composition of the sediment and underlying bedrock determines the nature and quantity of compounds that can be released under anoxic conditions (Boehrer & Schultze, 2008; Del Don et al., 2001). Additionally, Matzinger et al. (2007) suggest that meromixis is stimulated under a high rate of warming, which puts lakes at risk that lie in parts of the world that are experiencing rapid warming. Altogether, the likelihood of formation of meromixis with climate change is not obvious, and lake-specific approaches are necessary to evaluate this risk. Modelling efforts such as that by Matzinger et al. (2007) are a promising approach, which should be supplemented by lake-specific information on sediment release rates of major density-affecting solutes.

In summary, as a holomictic lake warms, the likelihood of incomplete mixing increases, especially under rapid warming rates (Matzinger et al., 2007). This creates an oligomictic regime, where the sawtooth pattern (Livingstone, 1997) may result in complete mixing in some years. This oligomictic regime increases the chance of anoxia and solute accumulation in the hypolimnion, potentially culminating in a sudden shift to meromixis (Figure 4b). Once a lake becomes meromictic, it might be difficult to reverse this change (Lepori et al., 2018). Lakes with the potential of strong solute release from the sediment and weak deep-water renewal are most susceptible to such a shift.

4 | CONCLUSION

Climate change can cause shifts in the mixing regime of deep lakes, which will change their behaviour in terms of physics, chemistry, and biology. In this study, we investigated whether certain feedbacks could affect these regime shifts. The investigated potential shifts are from polymictic to seasonally stratified, from dimictic to monomictic, and from holomictic to oligo- or meromictic. All these shifts in mixing regime display reinforcing feedback mechanisms, but these feedbacks are likely to be relevant under certain conditions only. In lakes of intermediate depth, polymixis and seasonal stratification can be alternative states, based on transparency and wind sheltering. If a period of stratification can trigger a strong reduction in transparency, for example due to phytoplankton bloom formation or release of CDOM, a stratified regime can form. However, this feedback is valid only under a narrow range of lake conditions, and the stratified state is not carried over from year to year, which is a full reset occurs each year. Dimictic lakes can become monomictic due to loss of ice cover. One study found that a shift from dimixis to monomixis could show bi-stability because of the ice-albedo feedback coupled to thermal heat capacity in sufficiently deep (at least 50 m average depth) lakes, but other studies in lakes and the sea suggest the opposite. The majority of studies would predict only a minor influence of memory effect of ice cover on lake dynamics, and therefore a gradual shift from mostly ice-covered to mostly ice-free winters. A climate-induced shift from holomixis to meromixis can occur if a density increase of the deep water layer by solute build-up outweighs a density decrease due to hypolimnetic warming. Such a shift would have profound influences on aquatic ecosystems, but more research is needed on this topic to assess where and when this can happen. If incomplete mixing does not result in a net density increase of the deep waters, an oligomictic regime is formed.

Although climate, interannual temperature variation, and morphometry are the main determinants of a mixing regime, transparency, water level, and internal feedbacks can facilitate and stabilise shifts between mixing regimes. Without denying the value of studies investigating mixing regime shifts driven by warming alone, we hope this paper places those findings in the perspective that several other components of lake ecosystems can influence mixing regimes as well. A change in mixing regime can mean a step-change in a physico-chemical parameter (e.g. anoxia) that can feed back to the vertical density distribution or heat budget. If we consider these processes as well, we may get a better understanding of how climate change affects lake mixing regimes. Given the great importance of mixing regime for functioning of lakes, more knowledge on the likelihood of transitions and the stability of such changes would be important for lake management. Observations of shifts in mixing regime due to internal lake processes are important, but may be hard to realise due to the long timescales and required data involved. For each of the three mixing regime shifts studied in this paper, modelling approaches have made important contributions. Inclusion of biogeochemistry in modelling could lead to further advances when investigating the shifts polymictic–stratified and holomictic–meromictic. The study of feedback loops in lake processes has so far been focussed mainly on shallow lakes (e.g. Scheffer, 1998). Our review is one of the first studies to systematically explore the potential feedbacks occurring in deep lakes, as well as the climate dependency of these mechanisms.

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DATA AVAILABILITY STATEMENT

Data sharing not applicable—no new data generated.

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