Meromixis in the Anthropocene: pathways of change

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Global warming is changing the thermal structure of lakes, creating longer and stronger periods of stratification, reducing winter cooling and shortening ice cover (Grant et al. 2021). Globally, surface water temperatures in lakes have risen since 1970, but trends in bottom water temperatures are less predictable and less pronounced on average (Kraemer et al. 2015; Pilla et al. 2020). As a result, thermal stability in HOLOMICTIC lakes has increased over the last decades, driving an earlier onset of stratification, oxygen consumption in the HYPOLIMNION, and longer periods of seasonal anoxia. Both models (see e.g., Woolway and Merchant 2019) and regional data syntheses suggest that one outcome of these changes will be development of MEROMIXIS (i.e. permanent stratification, generally with an anoxic MONIMOLIMNION – see BOX 1 for definitions). Equally, however, present meromictic lakes could be lost due to other global change processes: land-cover change and disruption of biogeochemical cycles are major drivers of lake change (Fig. 1).

The uncertainty about implications of loss or gain of meromictic systems hinges largely on the current lack of knowledge concerning these systems. As the number of meromictic lakes is not well constrained, it is impossible to estimate the extent of the potential loss. Woolway and Merchant (2019) predicted that <4% of their study lakes (n=635) would become meromictic, but importantly, they studied large lakes with an area >25 km^2. It is probable that small, relatively deep lakes will tend to dominate meromixis in the future, but even here the number of lakes that become permanently stratified may be limited because of the range of factors determining the development pathway (Fig. 1). In a regional, empirical assessment, Hakala (2004) estimated that in southern Finland, an area with a number of well-studied FERRUGINOUS lakes, 'only one lake in 800 is truly meromictic'.

We suggest that ecosystem functions and services of meromictic lakes and their global importance are equally poorly understood, and so the quality of what would be lost can also not be estimated. Current knowledge suggests that meromictic lakes should be protected, since they are especially vulnerable to environmental change (Hakala 2004). Without protection, we might lose unique model systems such as Lake Cadagno or Lake Mahoney that have been monitored for decades along with their unique microbiomes. Here we argue that the availability of meromictic lakes is threatened by anthropogenic change, and that the pathways leading to or away from meromixis involve more complex drivers than a simple change of water temperature. We illustrate possible future directions of change in meromictic lakes in the Anthropocene and consider their implications for future biogeochemical cycling. We focus on the fate of EUXINIC lakes and refer readers to Swanner et al. (2020) for a review of ferruginous systems.

Meromixis in the Anthropocene

Meromixis is a natural phenomenon that occurs on all continents and across a wide range of bioclimatic zones, ranging from tropical systems to isostatic rebound lakes (isolation basins) at both poles (Zadereev et al. 2017a). With the development of a permanent anoxic layer - the monimolimnion - there are profound changes in geochemical processes and formation of steep vertical biological and redox gradients (see below). However, a critical divide in the development pathways resulting in meromixis is that of water geochemistry: iron or sulfur dominance (Fig. 1), determining whether a lake becomes FERRUGINOUS or EUXINIC, respectively. This chemical composition in turn underpins the relative extent, rates and significance of associated biogeochemical processes and dynamics, and in some cases can be the predominant stabilizer of meromixis via density gradients. Furthermore, light penetration into the anoxic monimolimnion determines whether meromictic lakes, both ferruginous and euxinic, can become anoxygenic phototrophic systems (Fig. 1).

For many limnologists, meromixis is synonymous with stasis: long-term stratification with anoxia and its associated biogeochemical implications. The limited nature of monitoring data challenges this assumption: the key meromictic study sites have only been monitored for decades, and the loss of meromixis during routine monitoring has been observed. The question remains, how stable are meromictic lakes over time? Laminated lake sediment records and okenone (a carotenoid biomarker for purple sulfur bacteria [PSB] indicative of euxinic conditions) suggest that meromixis is temporally intermittent at many sites (e.g., (McGowan et al. 2008; Swanner et al. 2023) . However, neither laminated sediments nor the presence of okenone are uniquely indicative of meromixis. Moreover, shifts to enhanced stratification and meromixis under global-change processes will not be unidirectional (Fig. 1).

Climate forcing plays a major role in the development and maintenance of meromixis, but landscape setting (soils, geology, hydrology) and lake morphometry (size, fetch, hypsometry) can be critical for its development at local scales. Additionally, natural climate variability, and land-cover change (altered nutrient loads, primary production and hypolimnetic anoxia) impact development pathways (Fig. 1). Viewing meromixis simply as a product of changing lake thermal budgets is an over-simplification, particularly given the range and scale of anthropogenic drivers affecting lakes in the 21st century (Jenny et al. 2016). Eutrophication can result in BIOGENIC MEROMIXIS, if lake morphometry and landscape setting are conducive to its formation (e.g., Culver 1977; Hakala 2004). Anthropogenic and climate-driven hydrological alterations to regional freshwater-gradients promote ECTOGENIC MEROMIXIS, e.g. land-cover change altering runoff coupled with climate-driven evaporation (Hammer 1994; Jeppesen et al. 2020). In some areas, road salting is increasing salinity, reducing turnover events and promoting the transition from HOLOMIXIS to MEROMIXIS (Dupuis et al. 2019). These changes can create the necessary vertical density gradients leading to establishment and subsequent reinforcement of permanent stratification (Jellison and Melack 1993). The combined effect of these drivers suggests that the transition of many dimictic lakes to meromixis in the near future is inevitable. Conversely, human activities can also destroy meromixis: hydropower impoundments can reduce upstream saline water connectivity and replenishment (Bowling and Tyler 1986), while land-cover changes (e.g., clear-felling) that increase lake exposure and mean wind speeds, can work against vertical stratification gradients (Campbell and Torgersen 1980). As climate change is increasing air and lake-water temperatures, mean wind speeds are also rising, as well as the frequency of high energy storms, leading to an overall higher amount of energy in the earth system which reduces the stability of thermal stratification.

Anoxia and biogeochemistry in euxinic systems

EUXINIC meromictic lakes have been critical for understanding the processes associated with biogeochemical cycling in the early Earth system (Swanner et al. 2020). The dominant natural sulfur sources in groundwater and runoff stem from geologic weathering (and volcanic activity) but dry and wet S deposition has increased since the Industrial Revolution, and while regionally variable, can lead to increased deposition loadings. Inputs of sulfur also vary with agricultural use of S-containing fertilizers, an underestimated impact on lake chemistry in lowland landscapes (Zak et al. 2021). A further factor that can lead to elevated marine sulfate deposition is increasing storminess in coastal regions, which also notably impacts soil biogeochemistry (Monteith et al. 2023); associated reductions to DOC export have implications for the light and temperature climates of recipient lakes. In the following sections we discuss the possible impacts of pathways of change of meromixis (positive and negative) on selected key biogeochemical processes.

Anoxygenic carbon fixation

In euxinic lakes where sufficient light reaches a hydrogen sulfide-rich monimolimnion, characteristic bacterial layers composed of anoxygenic phototrophic purple and green sulfur bacteria (PSB; GSB) occur (Overmann 2008). Inorganic carbon fixation by these microorganisms can be a significant term in the carbon balances of such lakes), while below the photic zone in anoxic waters and sediments, sulfate reducing bacteria (SRB) and methanogens compete for electron donors such as hydrogen and acetate (Lovley and Klug 1986; Storelli et al. 2013; Block et al. 2021; Di Nezio et al. 2021). By intercepting nutrients, down-profile sulfurous bacterial plates represent barriers to their exploitation by mixolimnetic primary producers. However, although chemical gradients (O_2 / H_2S) may prevent access by most mixolimnetic heterotrophs to productive strata, they can also serve as a food resource to secondary producers. Shifts or loss of permanent stratification could consequently alter or obliterate such trophic links. Similarly, isolation of the monimolimnion means that it operates, to some degree, as a closed-system, where losses of CO_2 generated from OM degradation (albeit at low rates) are restricted, leading to lowered emissions and to accumulation, respectively (Fuchs et al. 2022). This stable stratification reduces nutrient transport across the chemocline, decreasing primary production rates, ultimately limiting the carbon sequestration potential of meromictic lakes, at the same time favouring carbon mineralization to methane (Tranvik et al. 2009). However, meromictic systems are highly sensitive to eutrophication - increased nutrient and DOC loading from the lake's catchment promotes primary production in the mixolimnion and associated light attenuation, effectively shading out PSB (Fig. 1).

Methanogenesis : In lakes with high organic loads, thermal stratification or incomplete turnover can promote anoxia and permissive redox conditions for CH_4 production. Methanogens, however, compete with sulfate-reducing bacteria (SRB) for fermentation products, particularly hydrogen (H_2), formate (HCO_2^-) and acetate ($C_2H_3O_2^-$). Where sulfate concentrations are sufficiently high, such as in euxinic lakes and their sediments, sulfate reduction is the dominant terminal electron-accepting process due to the higher energetic yield, and because SRB possess greater affinity for fermentation substrates by comparison with methanogens (Lovley and Klug 1986).

Although PSB are not directly involved in the methane cycle, their presence at the oxic-anoxic transition zone could contribute to the removal of CO_2 produced by methanotrophs. An interaction between oxygenic and anoxygenic phototrophs and aerobic methanotrophs could thus contribute to the oxidation of CH_4 in lake water, reducing its release to the atmosphere. As such, PSB could represent a very efficient methane filter by significantly reducing the upward flux beyond the chemocline (Milucka et al. 2015). Therefore, in the presence of PSB the predicted increase in meromixis may limit the release of CH_4 and CO_2 from lakes by sequestering these dissolved gases in the anoxic monimolimnion.

Biogenic volatile organic compounds (BVOC): BVOCs constitute a wide range of chemicals that can serve as signalling molecules and cellular protectants, provide energy and nutrients for microbes, and influence climate in various ways. Despite this, there is relatively limited information on lacustrine BVOCs concentrations and fluxes, and only occasionally is temporal and spatial variability considered. Most studies focus on one or a few of the hundreds of BVOCs, mostly on sulfurous BVOCs, whereas halogenated compounds, terpenoids, and oxygenated VOCs such as acetone, acetaldehyde and methanol, are studied much less commonly.

In euxinic lakes, the strong vertical gradients impact the BVOCs produced in the monimolimnion compared to those produced in the mixolimnion. In addition, salinity, temperature and even hydrostatic pressure differences can affect gas solubility. For example, fermenters and anaerobic respirers may provide distinct BVOCs to aerobes in the mixolimnion as by-products of their metabolism or as cellular protectants. The products of anaerobic metabolism can fuel communities in the chemocline and mixolimnion, which in turn may produce BVOCs that would be less abundant in deep holomictic lakes, creating a different volatile cocktail, some of which will escape from the lakes. This latter process is understood for methane and hydrogen sulfide, which feed a range of microbes, but less so for other volatile compounds.

Most research on BVOCs in meromictic lakes has focused on volatile organic sulfur compounds (VOSCs), which generally have a cooling effect on the atmosphere (Hopkins et al. 2023). Fritz and Bachofen (2000) measured VOSC concentration along the water column of meromictic Lake Cadagno, concluding that hydrogen sulfide, methanethiol, carbonyl sulfide, dimethyl sulfide, carbon disulfide, and dimethyl disulfide were biogenic, and that all except carbon disulfide (which also had the highest concentration) were restricted to the anoxic zone, with peaks in concentration at the chemocline. Thus, carbon disulfide, which can be microbially oxidized (Smith and Kelly 1988), may have an important and overlooked contribution to carbon and sulfur cycles, and indirectly to food webs in the mixolimnion, especially in and just above the chemocline. In the same way that anoxygenic phototrophs can use DMS as an electron donor and produce DMSO (Zeyer et al. 1987), it would be valuable to explore whether any can oxidize carbon disulfide.

The extent to which monimolimnia are excluded from gas exchange with the atmosphere is also uncertain (See discussion above on CH_4; although ebullition can clearly bypass chemo-/thermoclines). While the degree to which VOSCs are consumed will depend on the lake's physical status, with both direct effects on their flux and indirect effects by shaping microbial assemblages. For example, it may depend on the proximity of the chemocline to the lake surface, and thus whether the chemocline receives sufficient light to enable growth of anoxygenic phototrophs (Fig. 1). Factors such as ebullition and possible future loss of meromixis will also affect the release of VOCs from the anoxic zone into the atmosphere.

Carbon transfer between zooplankton grazers and anoxygenic phototrophs: Most studies on the biology of euxinic lakes focus on PSB and GSB and their importance for ecosystem functioning. The trophic relationships between these anoxygenic phototrophic bacteria and other members of the food web and the resulting energy flow remains relatively unexplored (Zadereev et al. 2017b). Toxic concentrations of H_2S can potentially preclude multicellular organisms including members of the zooplankton from feeding directly in the chemocline where PSB are concentrated. However, both calanoid copepods and *Daphnia* can reach higher densities in this zone and are often observed to be strongly red-coloured, which is thought to be caused by high concentrations of the respiratory haemolymph protein haemoglobin. The specific adaptations of the zooplankton necessary to survive under elevated H_2S concentrations are largely unknown, but an evolved tolerance towards higher H_2S concentrations for the brief time needed to move in and out of the chemocline could allow grazing under such conditions. Stable carbon isotope studies have provided evidence that the amount of PSB carbon transferred to the filter-feeding zooplankton can be as low as 5% in some lakes (Kankaala et al. 2010) but as high 85% in others (Overmann et al. 1999). An important intermediate position of nanoflagellates and ciliates between PSB/GSB and calanoid copepods or cladocerans including *Daphnia* has also been reported from some lakes (Jürgens et al. 1994; Taipale et al. 2009; Zadereev et al. 2017b), thus providing a trophic link between bacterial biomass production and secondary production in the mixolimnion. A possible disruption of these trophic connections might result from various aspects of global change: warming of the mixolimnion could generate deeper mixing and a consequently increased depth of the chemocline, where light levels might be insufficient to support phototrophic SB, ultimately leading to a strong decrease of in-lake carbon sequestration (Fig. 1). In naturally oligotrophic lakes, the loss of anoxygenic bacteria as direct or indirect food source could result in a strongly reduced zooplankton biomass with further consequences to nutrient availability, primary production and higher trophic levels, given the key role of the zooplankton in nutrient cycling (Vanni 2002).

Synthesis

To understand the pathways of change of meromixis and their implications for biogeochemical cycling, a first step will be to understand the typical characteristics and function of euxinic meromictic lakes in the Anthropocene. For example, can the two main model systems Lake Cadagno and Mahoney Lake (Gulati, et al. 2017) serve as representatives of all meromictic systems, including those presently holomictic lakes that modelling suggest will become meromictic? Other lake systems might be better models, such as the artificial pit lakes in various landscapes , or the low arctic, meromictic lake clusters embedded in a region with thousands of non-meromictic lakes in Southwest Greenland near Kangerlussuaq (Anderson and Stedmon 2007). Such landscape clusters of meromictic lakes are well suited to allow generalisations about natural meromictic lakes and their future (Hakala 2004). In addition to these, other model systems are needed to study the mechanisms of the loss of CULTURAL MEROMIXIS, as in Baldeggersee in Switzerland, an example for eutrophication leading to cultural meromixis, which was later reversed by aeration as a restoration measure (Wehrli et al. 1997). Paleolimnological studies, despite their limitations, help us understand the stability and natural variability of meromixis as well as contrasting development pathways. It is unclear how the changing light climate of lakes due to disruption of global biogeochemistry will interact with enhanced water column stability (Fig. 1). For example, eutrophication and regional increases in landscape DOM and Fe export (termed 'brownification' but mainly reflecting recovery from acid deposition) increase light attenuation (Thrane et al. 2014), which therefore could influence how future meromictic lakes function. Additionally, how will land-cover change and land-use intensification impact lakes that are presently meromictic? Finally, interactions between short-term extreme events (e.g., droughts; heatwaves; storm events; floods) and more progressive impacts (land use; temperature trajectories; nutrient and DOC exports) might accelerate or dampen the rates of pathways to change of meromictic lakes.

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Box 1: Meromictic glossary. Numbered references in Supplementary.

MEROMIXIS: We suggest that the term meromixis is reserved for lakes that are permanently stratified in the strict sense, echoing Hakala (2004)[1] [i.e., besides rare, stochastic mixing events[2]]. Classifications can mask the intricacies of individual systems: time and depth intervals of mixing, and terminology regarding initiation and reinforcement processes are sources of ambiguity that authors have highlighted and sought to resolve [1,3–8]**.** Two principal, non-exclusive categories are acknowledged:

[1] Endogenic meromixis can be **BIOGENIC**, reflecting salt accumulation in bottom waters due to organic matter sedimentation and degradation, which tends to develop in deeper and well-sheltered dimictic lakes and is typically initiated by unusual meteorological conditions that serve to reduce circulation. Initiation can be via an ectogenic event superimposed on drivers conducive to reinforcement of meromixis, such as eutrophication, or cryogenic meromixis, where salts frozen out of surface waters can accumulate in deeper waters. Transitions from meromixis to holomixis can occur with long-term reductions in depth due to sediment accumulation.

[2] Ectogenic meromixis may be short-lived, periodic, and stochastic, or more longstanding[9], and can have anthropogenic drivers such as land use change[10,11], de-icing road salts[12], mining, hydrological alterations to freshwater-marine connectivity[13], and hydropower development[14], also termed **CULTURAL MEROMIXIS.** Crenogenic meromixis[15] is generated by groundwater inputs to deep portions of lake basins.

EUXINIC meromictic lakes possess anoxic, hydrogen sulfide-rich monimolimnia. In general high levels of S and Fe do not co-occur under anoxic circumneutral conditions due to production of insoluble FeS.

FERRUGINOUS meromictic lakes possess anoxic, iron-rich monimolimnia; named for the presence of dissolved ferrous iron, rather than for a predominant contribution of iron to chemical stability, which can also be the case in some systems..

HOLOMICTIC lakes 'turn over' at least once a year to achieve water column chemical uniformity. Water density and stability is principally controlled by thermal regimes. General classification[6,16,17] provides further subdivision by mixing frequency and seasonal occurrence.

MONIMOLIMNION: The bottom strata of a permanently stratified water column, generally anoxic [*Monimo- (Gr.) permanent; fixed; steadfast*].

HYPOLIMNION: The colder, denser bottom strata of a stratified holomictic lake.

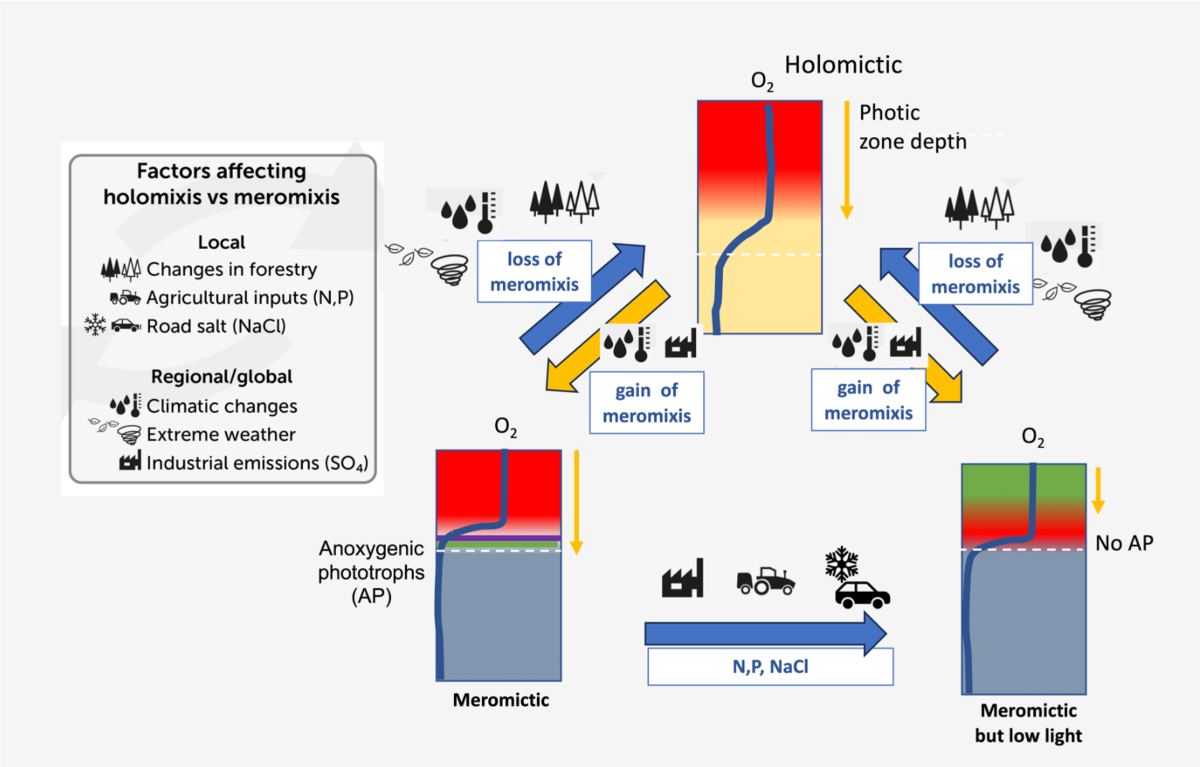

Figure 1. Schematic representation of the main pathways of future change in stratification from presently holo- and meromictic lakes. Broad differences in catchment-lake geochemistry will determine whether lakes become ferruginous or euxinic. Because the pathways of change are similar for both types of meromixis, we simplified figure to refer more generally to meromixis. However, changes in the water column transparency associated with other global change processes (notably, DOC load and eutrophication, both of which increase light attenuation) will determine whether anoxygenic phototrophic (AP) communities develop. The yellow downward yellow arrow indicates the depth of the photic zone and dashed white line the onset of hypoxia.

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Supplementary Material

Meromixis in the Anthropocene: pathways of change

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