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Ramesh D. Gulati
Egor S. Zadereev
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Ecology of Meromictic Lakes

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Preface

This book is not only a state-of-the-art book on Ecology of Meromictic Lakes but is also perhaps the first detailed published record focused exclusively on such lakes. Geller et al. (2011) had aptly remarked in the preface of a Springer book dealing with Acid Pit Lakes that most of these pit lakes appear to become meromictic during the course of their development. I (RDG) as one of the three editors of this book was very happy to get an invitation from Walter Geller late in 2012 to review their detailed book on the Acid Pit Lakes in the SIL newsletter. (This SIL newsletter is both a scientific and social forum for the limnologists and in fact all those interested in limnology the world over.) While reviewing the book on Acid Pit Lakes by Geller et al., it had struck me that meromictic lakes were an under-represented subject area of the lake limnology. My feelings were substantiated when I was invited by my Russian colleagues (Prof. Andrei Degermendzhi and Dr. Egor Zadereev, my co-editors of this book) to join them as a co-editor of this planned Springer book, the first one on the meromictic lakes. The most important task, also the most difficult one of choosing the book structure, was the format and chapter divisions and chapter authors. Both these aspects were taken care of by my Russian editorial counterpart (EZ and AD). Next, we decided to have the book to comprise three parts with 13 chapters.

The introduction (Chap. 1) is followed by Part I. Part I is a more general part including three concise chapters, one each on physical features, chemical features and the biology of meromictic lakes. These four chapters provide state-of-the-art information based on recent scientific literature on meromictic lakes. Strangely, we detected a striking bias in the expanse of scientific literature from Europe and North America with relatively the most literature on one hand and the remaining five continents with much less or no information.

Part II of the book has eight chapters, comprising scientific accounts of more than a dozen meromictic lakes, which are included here as case studies. The information ranges from one lake per chapter to several lakes in some other chapters. Chapter 12 that deals with lakes of a wide range of area, volume and magnitude in Mexico departs in style and contents from the preceding chapters.

This chapter is more of a critical review of the presence/absence of such lakes, with some information about meromictic lakes in the Mexico State, Central America. Unfortunately, information on the existence of meromictic lakes in countries on the main continent of South America is altogether lacking, let alone some data on the physico-chemical features or biology of such lakes. Much of the information in Part II is based partly on the published scientific literature and partly on the unpublished results. The authors of these Chaps. (5–12) are well known, having wide international experience on the limnology of meromictic lakes.

It was not an easy task to select lakes where the meromixis is supported by different processes and to cover various aspects of meromixis in the case-study chapters. We could not follow a geographical approach so as to cover all the continents. On the one hand, we tried to select meromictic lakes which have been comprehensively studied and, on the other hand, to include those lakes where research is ongoing. For example, we found in the literature that there were active studies in progress on microbiology of some meromictic lakes in Australia some years ago, but these lakes are being not so actively pursued anymore. At the first round of book preparation, we contacted a wider community of meromictic lake scientists. However, the final selection was also determined by the speed of response by the potential book authors and their desire to actively participate. Studies on meromictic lakes are intensively developed in several cases. For example, for Ace lake in Antarctica, recent, detailed publication on food-web structure appeared (Laybourn-Parry and Bell 2014) after we had already started with the preparation of the book. So, we realise that there are other important studies and well-studied meromictic lakes that are not included in the book as case study chapters. Nevertheless, we do refer to some such studies, e.g., on Lake Mahoney in Canada and Ace Lake in Antarctica in Chap. 4 on the biological aspects of meromictic lakes.

We feel that there are also some aspects of meromixis that probably should get more attention, but the researches on those topics are either ongoing or not well developed. Specifically, the hydrophysical and biogeochemical model predictions and simulations of regime shift from holomictic to meromictic conditions and vice versa (such shifts are described for Mono Lake in Chap. 11 and for Lake Rogoznica in Chap. 6) are extremely important from both the theoretical and practical limnology viewpoints. We discuss briefly in Chap. 9 that mathematical modelling is important for such predictions and enumerate some general considerations about the methodology of such simulations. This topic would require a separate chapter, but probably the researches on different lakes are not equally deep enough. We hope that this aspect will be studied more intensively in the near future, and the theoretical research on the stability of meromixis will improve our knowledge further on the mixing regime shifts in lakes.

Last of all, Part III of the book that deals with some General Conclusions (Chap. 13 by RDG and EZ) is derived partly from the summary conclusions provided by the authors of the foregoing 12 chapters to the editors.

Considering that it was our maiden attempt to edit a book on meromictic lakes, it was not always feasible to stick to the deadlines. Therefore, the preparation of the

book was delayed by some months. We also greatly appreciate the patience of the Springer staff (Andrea Schlitzberger and colleagues) dealing with the administrative part of the book preparation.

Last but not least, as Editors we are highly grateful to both the chapter authors (47 co-authors from 12 countries) and the reviewers for their cooperation and help.

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Chapter 1

Introduction: Meromictic Lakes, Their Terminology and Geographic Distribution

Egor S. Zadereev, Bertram Boehrer, and Ramesh D. Gulati

Meromixis has never really been main focus of the limnological research. However, many workers have felt the need during the last decades, and some recent scientific advances demonstrate the need to understand these meromictic lake ecosystems and their unique problems more thoroughly than hitherto. We cite here half a dozen instances, which support our contention to pay more scientific attention to what is already known of meromictic lakes:

- The disaster in 1986 at Lake Nyos, and Lake Monoun in 1984, both in Cameroon (Africa), where large amounts of CO₂ gushed out under pressure from deeper waters and escaped forcefully from the lake surface killing about 1700 people in the lake vicinity (Kling et al. 1987). We need understanding and theory to predict and minimise probability or consequences of such catastrophic events.
- Opencast mining now in progress leaves depressions, which get filled with water. Many of these lakes tend to become meromictic, i.e. they do not circulate completely. To assess the water quality in such lakes, we need to understand the mechanism of meromixis (Böhrer et al. 1998; Schultze et al. 2016). We know that some lakes have been turned meromictic on purpose to improve surface water quality (e.g. Island Copper Mine, Canada: Fisher and Lawrence 2006).
- It is planned to exploit the rich methane deposits in deeper waters of meromictic Lake Kivu bordering the Democratic Republic of the Congo and Rwanda in Africa for power production without letting the surface waters to deteriorate. To

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minimize the environmental impact, transport processes for gases must be understood.

- Climate change might impact the stability of stratification and circulation patterns in many lakes and hence the lake food webs and ecosystems (Danis et al. 2004). In some cases, anthropogenic influences turn holomictic lakes to meromictic ones (e.g. Mono Lake: Melack and Jellison 1998; see also in Chap. 11). If a lake shifts to another mixing regime, the food web and biological communities are stressed. To predict and understand the response of ecosystem to altered mixing regime, comparative studies of meromictic and non-meromictic lakes are needed.
- Lake sediments from meromictic lakes represent some of the best climate records, which range from a few hundred years to more than ten thousand years. Moreover, the paleolimnological studies tell us a lot about the past climate and thus improve our understanding about meromixis.
- The different chemical settings in meromictic lakes support diverse microbial processes concerning carbon fixation and oxidation. A very obvious example is the anoxygenic photosynthesis by phototrophic sulphur bacteria. Examples that are more specific are the anaerobic oxidation of ammonia (Anammox) by obligately anaerobic chemolithoautotrophs or primary production by photoferrotrophic bacteria. Studies on these bacteria can provide us with a more all-inclusive understanding of different primary production processes and have high biotechnological value.

1.1 Terminology

We follow Hutchinson's definition of meromixis: "A lake in which [a chemically different] water remains partly or wholly unmixed with the main water mass at the circulation periods is said to be *meromictic*. Findenegg (1935), who introduced these terms, called the deep layer of a meromictic lakes the *monimolimnion*, and Hutchinson (1937) introduced the term *mixolimnion* for the part above the monimolimnion in which free circulation periodically can occur. The boundary layer between the mixolimnion and the monimolimnion is known as the *chemocline*" (Hutchinson 1957, for details see Chap. 2). With only some modifications, this definition still holds after 60 years.

It was necessary to add *a chemically different* at the beginning of the definition, as Hutchinson (1957) took for granted that lakes without full circulation would develop pronounced chemical gradients: he thus defined the transition between mixolimnion and monimolimnion as "the chemocline" and considered the monimolimnion as stagnant layer. In 1957, it was not known about the lakes that are permanently stratified but do not develop a pronounced chemical gradient. This comprises deep lakes with thermobaric stratification (stable density stratification which results from the temperature dependence of the compressibility of water; see Bohrer et al. 2014 for details) and lakes that generate deep water by partial deep-

water renewal (e.g. Issyk-Kül: Peeters et al. 2003). Referring to chemical gradients in the definition also clearly distinguishes between meromictic lakes and oligomictic lakes (which experience a complete overturn once every few years—without developing a pronounced chemical gradient, e.g. Lago Maggiore: Ambrosetti and Barbanti 1999). Strictly speaking, here we depart from defining the term *meromictic* as opposite of the *holomictic* (see Hall and Northcote 2012).

If intervals of no overturn result in intermittent chemical deterioration of the deep water, it is prudent to call it a meromictic period or phase (e.g. Melack and Jellison 1998 and Chap. 11). Therefore, we removed the word “perennially” from the definition. This also confirms that we know that monimolimnia can vary in age (e.g. Kaden et al. 2010) and that its water and solutes are exchanged with the overlying mixolimnion. Consequently, monimolimnetic water can be younger or newer in existence than the meromixis in the lake (e.g. Vollmer et al. 2002). We have also eliminated the word “stagnant”, as we know that there is also motion in the deep-water layers determined by the pressure differences with the surface waters and drag (fluid resistance) between layers. Monimolimnia receive inflows from the groundwater (crenogenic meromixis—see below), but also monimolimnetic water can creep into the groundwater space. Beyond this, also macroscopic vertical circulation within monimolimnia has been documented, e.g. by double diffusive convection—a form of convection driven by two different density gradients, which have different rates of diffusion (Newman 1976; Imboden and Wüest 1995), which also has been confirmed for temperate lakes (von Rohden et al. 2010) and which can comprise the entire monimolimnion in one convection layer without breaking or even terminating its meromictic nature (Boehrer et al. 2009).

Protected against direct gas exchange with the atmosphere, oxygen-depleting processes overcome oxygen production in the very low-light or dark conditions of monimolimnion. Thus, the redox potential becomes more negative in the monimolimnion, which is usually anoxic. This creates a special setting for chemical gradients in meromictic lakes, which can be colonized by diverse microzooplankton and microbial communities (see Chap. 4).

The classification of meromictic lakes by Hutchinson (1957) is based on processes that initiate the density stratification. This classification differentiates ectogenic, crenogenic and biogenic meromixis, i.e. meromixis caused by external inflows, entry of groundwater and degradation of organic material, respectively. Later, Walker and Likens (1975) refined Hutchinson’s classification into two groups of ectogenic and endogenic meromictic lakes: ectogenic meromictic lakes remain permanently stratified due to inflow of different solute concentration, inflow of high turbidity or inflow of groundwater of higher salinity. Endogenic meromictic lakes are formed either by degradation of organic material in the deep water or by salt exclusion when ice is formed during winter. Hakala (2004) recognized meromixis that results from (1) flow/precipitation of saline water over freshwater or the other way round; (2) superficial diffuse nutrient load or turbidity currents, or both, from the catchment; (3) subsurface inflow of groundwater; and (4) inadequate mixing due to the lake morphology and surrounding topography. Boehrer and

Schultze (2008) listed all processes that are said to sustain meromixis (see also Chap. 2) and reasoned that as soon as meromictic conditions are established, more processes can be activated that contribute to keeping the stratification stable. Many lakes hence do not belong to just one class. Boehrer and Schultze (2008) conclude that all sustaining processes must be considered collectively. As long as these processes can balance mixing and diffusive effects that erode the stratification, the lake will remain meromictic. In Chap. 2, all the processes that have been documented to form and sustain meromixis are divided into two groups: (1) those which operate purely mechanically and (2) those in which geochemistry of lake waters is a controlling factor. It is important to recall that organisms also regulate many geochemical processes.

Meromixis traditionally has been regarded as a permanent setting. In some lakes, e.g. in Lake Salsvatn (Norway) (Bøyum 1973) and Powell Lake (Canada) (Sanderson et al. 1986), deep water was sealed off since the end of the last ice age. However, recent scientific contributions have shown a more dynamic picture of meromixis. Monimolimnia get eroded by mixing effects (e.g. Wallendorfer See and Rassnitzer: Boehrer et al. 2014); also seasonal variation in chemocline location has been quantitatively tracked (e.g. von Rohden et al. 2009; Zadereev et al. 2014; Nixdorf and Boehrer 2015). Holomictic lakes can turn meromictic due to climate change, and hence a new hydrologic situation can occur as for Lake Van, Turkey (Kaden et al. 2010), or due to the combined effect of climate and anthropogenic impacts (Lake Ikeda, Japan: Boehrer et al. 2008). On the other hand, such phases can also terminate (e.g. Dead Sea: Nissenbaum 1969; Imboden and Wüest 1995; Lake Mono: Melack and Jellison 1998). Hakala (2004) even regarded meromixis as a typical phase of lake formation on the Aland islands in the Baltic. Even if stratification is sustained continuously, exchange between mixolimnion and monimolimnion can occur by mixing across the chemocline, by seasonal progression and recession of the monimolimnion and by partial deep-water renewal (see Chap. 2). Hence, the age of monimolimnetic water does not necessarily have to comply with duration of the meromixis (e.g. Vollmer et al. 2002).

Finally, classifying a lake as meromictic has to be done carefully. It is clear that regular sampling during different seasons should confirm the presence or absence of mixing. Moreover, to classify a lake as meromictic, based on mixing regime (e.g. as dimictic or holomictic) is here not our aim per se. The lake once classified as meromictic can switch to another annual circulation pattern. Also, the age of monimolimnetic waters can be much younger than the duration of meromixis. What is relevant is to understand the current circulation pattern in the lake (e.g. meromixis during a specific time period, annual mixing, etc.) and based on regular monitoring either reaffirm it or refute it.

1.2 Worldwide Distribution of Meromictic Lakes

Hall and Northcote (2012) refer to the global distribution of meromictic lakes. They recognize 177 meromictic lakes on the Globe, located in nine geographical regions on five continents, with South America excluded. It is not surprising that most meromictic lakes are reported from North America (79 lakes) and Europe (28 lakes), since limnological studies are much more intensive and well recorded in these two continents. Interestingly, a recent review of 365 lakes with hypoxia (some of them are meromictic) by Jenny et al. (2016) appears to be also geographically biased: most lakes with hypoxia are also found in Europe and North America.

Presumably, the number of meromictic lakes is much higher if we also carefully investigate lake meromixis in other parts of the world. Aptly, although Hall and Northcote (2012) found information for only nine meromictic lakes in Asia, we assume that many more meromictic lakes exist in the arid and huge mountainous regions of Asia. For example, recently Dr. Rogozin (pers. com.) who regularly sampled Lake Uchum (South Siberia, Russia), which is located close to meromictic lakes Shira and Shunet in Siberia (see Chap. 5), found that Lake Uchum was not mixed at least during the 1-year field study. Rogozin believes that this lake, based on its size, salinity, morphology, geography and the laminated sediment, is meromictic. Hall and Northcote (2012) found no evidence from the literature on the presence of meromictic lakes in South America. In South America, however, we discovered the existence of meromictic pit lake at the Kori Kollo Mine, Bolivia (see Chap. 9). Also, literature search reveals references to a small (15 ha) and deep (45 m) meromictic lake Laguna El Ocho (3250 m a.s.l.) situated about 80 km south-east of Santiago, Chile, in South America (von Gunten et al. 2009).

Anderson et al. (1985) documented about 160 lakes in North America: they are all meromictic and (or) have a laminated sediment. Such a sediment is generally considered as typical for meromictic lakes. Indeed, meromictic lakes are not mixed down to the bottom. Also, they lack benthic organisms in their monimolimnion or in their anoxic bottom sediment. Obviously, the laminated sediment is formed not necessarily in meromictic lakes but also if conditions in the lake in and above the sediment do not lead to bioturbation (Scharf et al. 2010; Wendt-Potthoff et al. 2016). Some lakes in the list of Anderson et al. (1985) appear obscure, especially those reported as “seasonally meromictic” or if “they overturn occasionally”. Nevertheless, the authors list some 100 lakes that are known to be, or are likely to be, meromictic.

In this book, we discuss either in detail or refer to published studies on 83 meromictic lakes located in five of the six continents (Fig. 1.1). It is interesting to contemplate about the global distribution of meromictic lakes and the potential mechanisms that support meromixis and geographical areas or climate regions where these mechanisms are conceivable. There is a resemblance between the map on the distribution of meromictic lakes mentioned in this book (Fig. 1.1) and the map of the worldwide prevalence of saline lakes (Williams 2002). Some meromixis sustaining processes are linked to the salt content, e.g. the salt exclusion during ice formation (see Chap. 2). Such a mechanism supports meromixis in

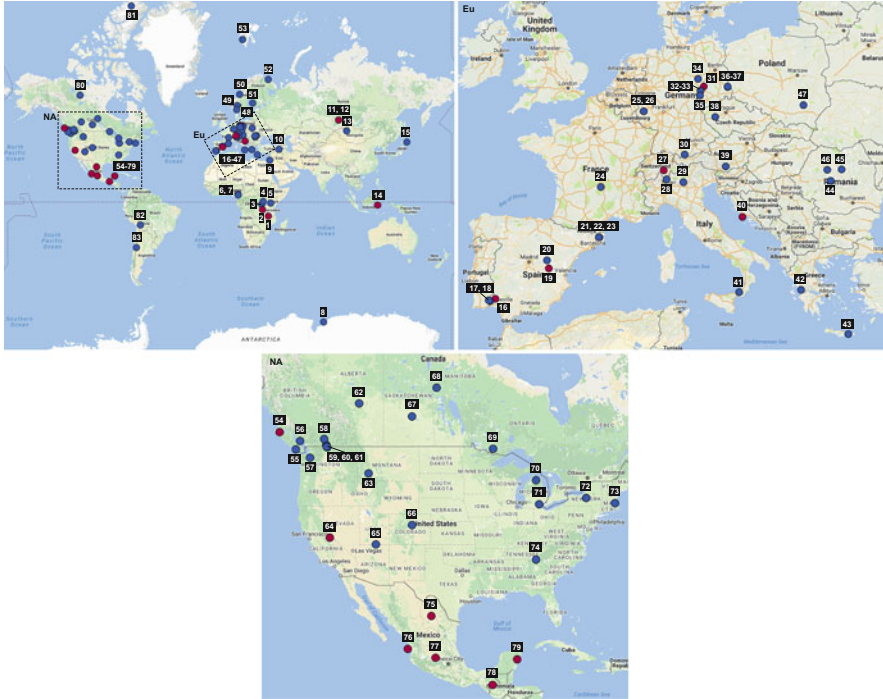


Fig. 1.1 Global distribution of meromictic lakes mentioned in this book on ecology of meromictic lakes. *Red dots*—lakes described in Special Study chapters (Part II of this book). *Blue dots*—lakes mentioned in different chapters of this volume. This map is available online at <https://www.google.com/maps/d/embed?mid=16dUc71xcIaoLb0WdFIYG7QmQNYM>. The list of continents and lakes: **Africa**: 1—Lake Malawi (Chap. 10), 2—Lake Tanganyika (Chap. 10), 3—Lake Kivu, 4—Lake Nyahirya, 5—Lake Sonachi, 6—Lake Nyos, 7—Lake Monoun; **Antarctica**: 8—Ace Lake; **Asia**: 9—Dead Sea (was meromictic before 1979), 10—Lake Van, 11—Lake Shira (Chap. 5), 12—Lake Shunet (Chap. 5), 13—Oigon Lake, 14—Lake Matano (Chap. 10), 15—Lake Harutori; **Europe (EU)**: 16—Cueva de la Mora (Chap. 9), 17—Nuestra Señora del Carmen Mine Pit, 18—Gudiana Pit Lake, 19—Laguna de La Cruz (Chap. 8), 20—El Tobar Lake, 21—Lake Banyoles, 22—Lake Ciso, 23—Lake Vilar, 24—Lake Pavin, 25—Schalkenmehrener Maar, 26—Weinfelder Maar, 27—Lake Cadagno (Chap. 7), 28—Lake Lugano, 29—Lake Idro, 30—Lake Alatsee, 31—Lake Goitsche (Chap. 9), 32—Rassnitzer See, 33—Wallendorfer See, 34—Felsensee, 35—Lake Vollert-Süd, 36—Lake Waldsee, 37—Lake Moritzteich, 38—Hromnice Lake, 39—Längsee, 40—Rogoznica Lake (Chap. 6), 41—Lake Faro, 42—Aitoliko Lake, 43—Salty Lake, 44—Fara Fund Lake, 45—Ursu Lake, 46—Ocnei Lake, 47—Piaseczno reservoir, 48—Rørholtfjorden, 49—Nordbytjernet, 50—Salsvatn, 51—Lake Alinen Mustajarvi, 52—Lake Mogilnoe, 53—Kongressvatn; **North America (NA)**: 54—Island Copper Mine Pit Lake (Chap. 9), 55—Nitinat Lake, 56—Sakinaw Lake, 57—Hall Lake, 58—Brenda Mine, 59—Lake Mahoney, 60—Blue Lake, 61—Hot Lake, 62—Roi Lake, 63—Berkeley Pit, 64—Mono Lake (Chap. 11), 65—Powell Lake, 66—Soda Lake, 67—Waldsea Lake, 68—Camp Lake, 69—Caland pit lake, 70—Hemlock Lake, 71—Third Sister Lake, 72—Fayetteville Green Lake, 73—Lower Mystic Lake, 74—South Mine pit lake, 75—Cuatro Ciénegas (Chap. 12), 76—Isabela Lake (Chap. 12), 77—Rincón de Parangueo (Chap. 12), 78—Dos Lagos (Chap. 12), 79—Nohoch Hol (Chap. 12), 80—Zone 2 Pit Lake, 81—Lake A; **South America**: 82—Kori Kollo Mine, 83—Laguna El Ocho

Siberian, e.g. lakes Shira and Shunet (Chap. 5), and in Canadian meromictic lakes (e.g. Lake Mahoney: Northcote and Hall 1990). Thus, areas where the saline meromictic lakes are supported by similar mechanisms are in dry regions where evaporation exceeds precipitation, with severe cold climate as in Siberia or parts of Canada.

Saline lakes in general are quite susceptible to the effects of climate change, as both lake volume and salinity and its gradients depend on the hydrologic condition. For example, Aral Sea has significantly declined in volume during the last 60 years or so. This water-level decline has resulted in a dramatic salinity increase. The Western Large Aral Sea has now a very strong halocline between 6 m and 8 m depth that reminds us about the situation typical of meromictic salt lakes (Izhitskiy et al. 2016). Thus, we expect meromictic lakes to occur in regions with saline lakes after a drop of water level (drought, water diversions, any other natural or anthropogenic factors that accelerate the water-level drop in saline lake) or in dry territories with saline lakes after the superficial freshwater runoff due to ice melt and accidental heavy rains, if there is flow of freshwater.

Recent predictions reveal that the effect of climate change will cause salinization of many lakes in Mediterranean climate zone (Jeppesen et al. 2015). Lewis et al. (2015) demonstrated that the subarctic lakes in Alaska are shrinking with the substantial increases of nutrients and other ions which lead them to become eutrophic or saline. Another causal factor for salinization of many inland lakes is water from salt applied to roads in winter. Kelting et al. (2012) demonstrated that the concentration of sodium and chloride ions in lakes within the watershed of US national roads is positively correlated with the density of roads and the extent of salts applied in wintertime. Sibert et al. (2015) recently described the effect of road salt on the chemical stratification of an urban lake as *cultural meromixis*. Thus, many factors, including both natural and anthropogenic, can augment the salinity of many freshwater lakes and under favourable circumstances turn such lakes to become meromictic.

Some small meromictic lakes are located in karst areas where deep vertical holes are filled with water. When such holes are located close to the sea, the saline water is either trapped in the holes or can infiltrate the system through the ground. In both cases, meromixis can be established and sustained long. The maps of global distribution of carbonate rocks, which usually overlap with karst areas, reveal that these rocks are widespread over the world (Ford and Williams 2007) and some meromictic lakes mentioned in this book are located exactly in the karst areas, e.g. Lake Rogoznica, Chap. 6; Laguna de La Cruz, Chap. 8; and Mexican meromictic lakes, Chap. 12. Probably many small karst holes filled with water have not yet been investigated but appear to be meromictic.

Many meromictic lakes are, indeed, man-made lakes established in former surface mines deep enough to intersect the local water table, so-called pit lakes (see Chap. 9). Usually such lakes have a steep lake basin that prevents mixing in the water column. The geochemical variability of water within the pit lake catchment (i.e. total dissolved solids, chemical composition, pH) also plays an important role in stratification. The number of such pit lakes is rising worldwide because mine pits are abandoned after

exploitation and flooded and new open pit mines are excavated (Castendyk and Eary 2009). The geological setting for different minerals varies. Hence the chemical characteristics of mine pit lakes also depend on the materials mined (rock quarries, gravel, kaolinite, sulphur, lignite, coal and metal ore mines). In general, mine pit lakes are more prone to show meromixis than natural lakes (Schultze et al. 2016).

Global distribution of meromictic lakes can be partly explained by the global and regional conditions that favour the development of meromixis. However, several natural and anthropogenic factors can affect the territorial patterns of meromixis. It is, therefore, difficult to map the presence of all meromictic lakes because some lakes will lose meromixis, while others may turn from holomictic to meromictic. Regular monitoring is the key to track the condition of many lakes and classify their current mixing regimes.

1.3 Introduction to This Volume

Currently, there are no books devoted exclusively to meromictic lakes. The information on meromixis in limnology textbooks is often short and fragmentary (e.g. Kalff 2003) and the account on meromixis in the thematic chapter in the Encyclopedia of Inland Waters (Stewart et al. 2009) does not appear to be sufficient in many respects. However, there has been great progress regarding our understanding of meromixis more recently that we cover in our book. This includes the mechanisms of stabilization of meromixis, details of the biogeochemical and ecological processes involved in meromixis. Data and measurements that are more accurate are available and span over time periods that allow a better description of processes controlling meromixis in lakes. Now, limnology can provide quantitative data on issues connected with meromixis. With this book, we comply with the need for a comprehensive collection of data and studies on meromixis.

In this book we refer to 83 meromictic lakes located in five continents excluding Australia (Fig. 1.1). There are too many meromictic lakes and the variability among them is too large to include all in this book. We select a few prominent cases that are also instructive for our general understanding. In Part I of this book, we discuss information on salient features of meromictic lakes, focusing on physical (see Chap. 2), chemical (see Chap. 3) and biological (see Chap. 4) properties of these lakes. The Case Study chapters in Part II (Chaps. 5–12) are each dedicated to one particular meromictic lake or a group of such lakes. There are chapters on meromictic karst holes and pit lakes and large meromictic lakes located in hot tropical region and, and contrasting these, small and saline meromictic lakes in the cold and generally dry Siberian climate. Chapter 13 highlights in brief the Conclusions based on the summaries of the preceding 12 chapters. Hence, we hope to provide guidance to the reader to collate detailed information of single lakes. We hope this book will provide a practical guide to meromictic lakes for limnologists.

Several study aspects covered in this volume differ from those in the existing literature on meromictic lakes mainly in:

- (a) Detailed studies on different meromictic lakes with mechanisms that cause and sustain meromixis in such lakes
- (b) Reviews of information on the food web structure and on organisms adapted to meromictic conditions, especially microorganisms forming the microbial food web and how this food web is connected with macrobial or the major food web
- (c) Description of meromictic lakes as paleolimnological archives due to preserved layers of intact sedimenting material in these lakes during meromictic conditions and the presence of specific paleolimnological markers (e.g. markers of purple sulphur bacteria, or the so-called PSB)
- (d) Updated information on bacterial diversity in the meromictic lakes supported by molecular biology techniques and information on microbial processes, including those not adequately covered in earlier literature, such as anaerobic methane oxidation, anaerobic ammonium oxidation and sulphate reduction at low pH.

It is, however, not possible to answer all questions on ecology of meromictic lakes. There are some uncertainties regarding terminology of meromixis; moreover, we believe that many meromictic lakes are still undiscovered. Most probably, the discovery of new meromictic lakes in extreme habitats or with specific thermal, chemical and biological regimes will bring new knowledge on the functioning of biological communities. Rather than the final answer, we consider this volume as a relatively comprehensive update reference that can be used in the future studies on meromictic lakes.

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Part I
Special Features of Meromictic Lakes

Chapter 2

Physical Features of Meromictic Lakes: Stratification and Circulation

Bertram Boehrer, Christoph von Rohden, and Martin Schultze

2.1 General Features

In meromictic lakes, a chemically different deepwater layer “the monimolimnion” remains perennially as a consequence of insufficient mixing with the overlying water body “the mixolimnion” (e.g., Findenegg 1933, 1935, 1937; Hutchinson 1937, 1957; Boehrer and Schultze 2008).

The transition between *mixolimnion* above and *monimolimnion* below is called the *chemocline*, as many chemical conditions change over a short vertical distance (Hutchinson 1957). Usually higher concentrations of solutes in the monimolimnion and stable density stratification are sustained throughout the annual cycle. In most cases, a high density gradient restricts the vertical exchange of water parcels and hence the turbulent transport of dissolved substances as well as heat. As a consequence, strong chemical gradients are conserved, and a fine zonation in this depth range can establish. Scientists looking at different features of the chemocline (gradients of electrical conductivity, oxygen, organisms, etc.) refer to slightly different depth ranges within this zone when speaking of “chemocline” (see Fig. 2.1).

The mixolimnion shows stratification and circulation patterns as in holomictic lakes, i.e., lakes without a monimolimnion, with the usual vertical subdivision into epilimnion (upper layer) and hypolimnion (lower layer). At the end of the thermal stratification period, deep recirculation mixes both layers. A lake (or the

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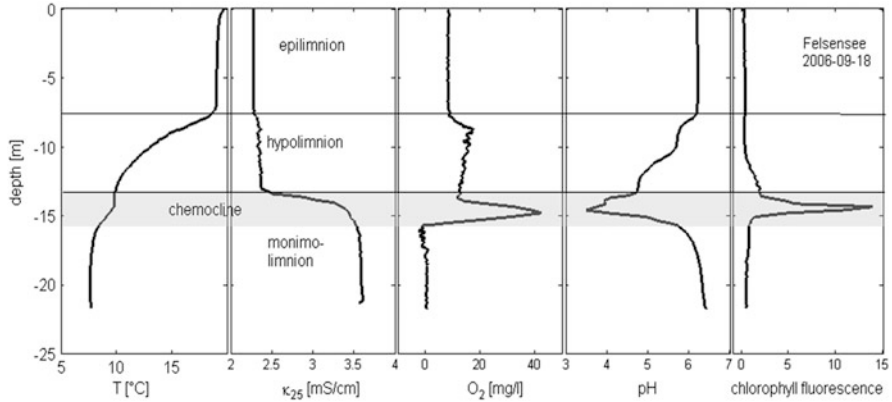


Fig. 2.1 Profiles of temperature, electrical conductance, oxygen concentration (numerically corrected for sensor response time), pH and fluorescence of the chlorophyll against depth in Felsensee (near Magdeburg, Germany). The *upper horizontal line* indicates the interface between epilimnion and hypolimnion, while the *lower horizontal line* marks the interface between hypolimnion and chemocline

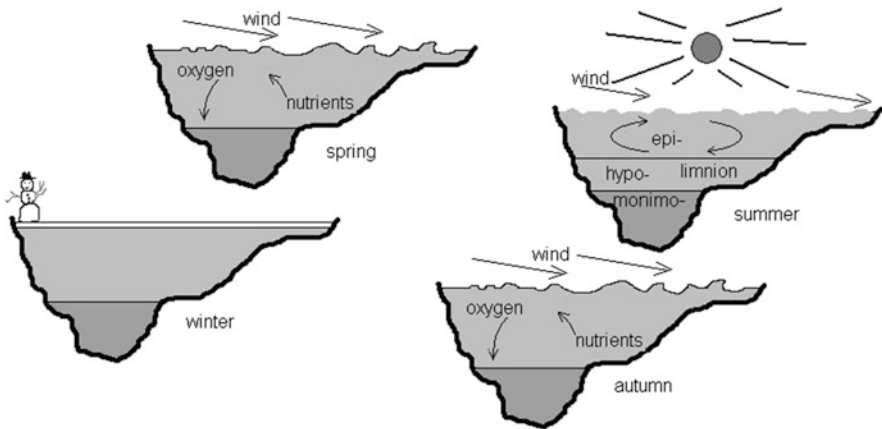


Fig. 2.2 Sketch of stratification and recirculation in a meromictic lake over an annual cycle

mixolimnion of a meromictic lake) can be monomictic (one recirculation period during the cold season) or dimictic (with a deep recirculation during spring and autumn—see Wetzel 2001—over an annual cycle depending on the climate zone; Fig. 2.2).

Similar to deeper holomictic lakes, a water layer at the surface heats up in spring as a consequence of increased solar irradiation and contact to a warming atmosphere. As a consequence, warmer water is formed, which floats on colder, denser water. While the upper layer, the epilimnion, is exposed to gas exchange and energy transfer with the atmosphere all year round, the hypolimnion below is shielded from

direct impact during summer. Usually the hypolimnion remains density stratified over the summer stratification period. Hence, vertical exchange of water parcels requires energy, which is available only in a limited amount. As a consequence, vertical transport of solutes and heat is small during stratification periods.

Over the summer stratification in the mixolimnion, little is happening about the depth of the chemocline. Groundwater may enter the monimolimnion and contribute to its volume, and hence the chemocline slowly rises (von Rohden et al. 2010). In addition, diffusion and turbulent transport of solutes from the monimolimnion can raise the density gradient locally and lead to oxygen demand in the lowest zone of the hypolimnion. Affected water may change its properties from hypolimnetic to monimolimnetic and eventually become a part of the monimolimnion. An ice cover can add another period of quiet conditions (winter stagnation). In latitudes where ice cover extends for a long period, this can result in meromixis (e.g., lakes Shira and Shunet, Chap. 6), as the subsequent circulation in spring time is short or is completely missing. The ice cover together with the quick warming up due to high concentrations of colored humic substances (Eloranta 1999), basin shape, and an almost complete protection from wind probably cause high frequency of meromixis in the small, humus-rich forest lakes in Finland (Merilainen 1970; Salonen et al. 1984).

Later in the year, cooling at the lake surface removes the protecting thermal density stratification, and convection forces water motion down to the chemocline. Turbulent kinetic energy is used to shave off parts of the chemocline. As a consequence, the chemocline moves downward and gradients get sharper. The upper part of the monimolimnion gets included in the mixolimnion and so do the water and chemicals contained in it. This is of particular interest for nutrients available at higher concentrations in the monimolimnion. The volume of water introduced into the mixolimnion depends on weather conditions during the recirculation periods and may, therefore, greatly vary from year to year. The deeper monimolimnion remains unchanged as long as its density is greater than that of the mixolimnion and it is sufficient to withstand the erosion by advected and locally produced turbulent kinetic energy.

Typically meromictic lakes show increasing electrical conductance with depth because of increasing concentrations of ionic solutes with depth. In general, higher concentrations of solutes increase the density of water (see below paragraphs on density). Due to mixing at least once each year, differences between epilimnion and hypolimnion are small. However, gradients between mixolimnion and monimolimnion can be enormous. Gradients are known to range from salinity under freshwater conditions to salt concentrations exceeding beyond salinity in ocean water (Wallendorfer See, Germany; Boehrer et al. 2014) or exceeding 100 g/L as in hypersaline meromictic lakes (e.g., Hot Lake, USA; Zachara et al. 2016; see also Chap. 3).

Temperatures at the lake surface are determined by weather conditions, while in the hypolimnion, one usually finds temperatures prevailing during the last cold period (e.g., Boehrer et al. 2000). In lakes located in colder climates, hypolimnion temperatures are close to the temperature of maximum density under normal

conditions (i.e., 4 °C for freshwaters but slightly lower at high salinities). Interestingly the monimolimnion is locked between hypolimnion above and ground/groundwater below. While its upper boundary is defined by temperatures during the cold period of the year, the lower boundary is warmer due to groundwater reflecting more an annual average temperature and geothermal heat flux. Usually a monimolimnion has a temperature gradient that reduces the density gradient imposed by dissolved substances.

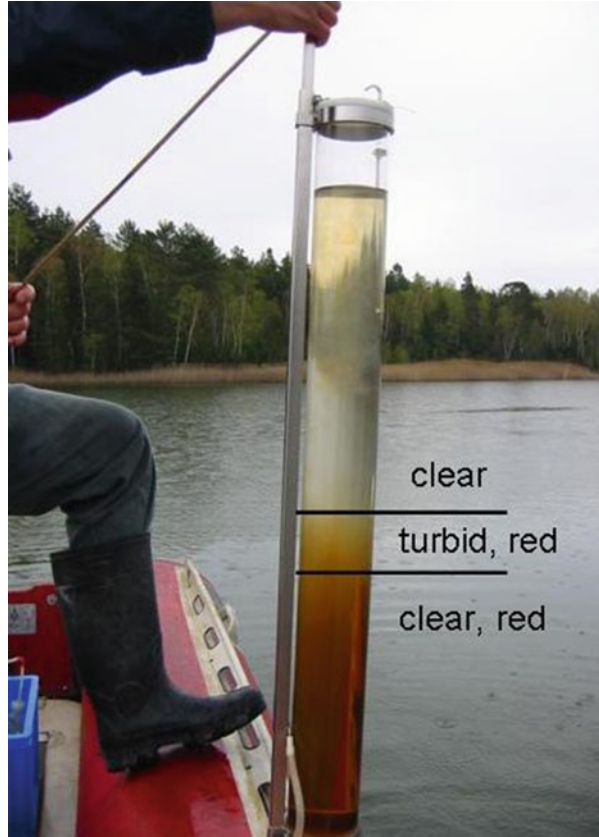
Both, the permanent density stratification in the deep water and the seasonal circulation of the mixolimnion, determine the distribution of solutes, as we show for oxygen as one of the key solutes for organisms. At the water surface, the atmosphere implies the boundary condition for oxygen. As a consequence, the epilimnion usually shows oxygen concentrations close to the equilibrium with the atmosphere, i.e., close to 100 % saturation (by definition) at the respective temperature. The hypolimnion can have higher concentrations of oxygen than the epilimnion due to higher solubility of oxygen at lower temperatures during the last mixing period or due to photosynthesis, if the light penetrates to deeper layers. However, over the stratification period, oxygen in the hypolimnion is subject to depletion until the next circulation period when the oxygen levels are recharged. Oxygen concentrations drop to zero across the chemocline. The extent of availability of oxygen sets the conditions for the fate of other solutes. As the contact line between water masses of different chemistry, the chemocline is a zone of active chemical transformations (see Fig. 2.3). Consequently, organisms have to cope with the chemical conditions in this gradient zone. Some organisms manage to profit from unusual chemical conditions (see Chap. 4).

2.2 Processes Forming Meromixis

In general, water density is higher in the monimolimnion than in the mixolimnion so as to retain the monimolimnion throughout the year. To balance the gradual reduction of this density difference by diffusion and mixing, a process is required that transports substances into the higher concentration waters of the monimolimnion.

Hutchinson (1957) classified meromictic lakes according to the major processes that transport solutes. He could identify three classes, (1) ectogenic, (2) crenogenic, and (3) biogenic meromixis, i.e., meromixis caused by (1) external inflows, (2) groundwater, or (3) degradation of organic material, respectively. On a broader base of examples, Walker and Likens (1975) refined Hutchinson's classification into groups when lakes remain permanently stratified due to (1) inflows of different salinity, (2) inflows of high turbidity, or (3) inflowing groundwater. These three groups comprise ectogenically meromictic lakes (class A), while endogenic meromixis (class B) is formed either by (4) degradation of organic material in the deep water or (5) by salt exclusion when ice is formed during winter.

Fig. 2.3 Water sample from about 10 m depth from Moritzteich (south of Berlin, Germany), showing the transition from colorless water of mixolimnion (*upper* part of the sampling tube) to red water of monimolimnion (from Boehrer 2013). The turbidity in the chemocline is the result of oxidation and precipitation of iron



Since these cited works on classification of meromictic lakes, many meromictic lakes have been scientifically investigated and reported. Microbiologically controlled chemical reactions, e.g., iron meromixis (Hongve 2002), have been understood more in detail, and their contribution to the density of monimolimnetic waters can be evaluated (e.g., Dietz et al. 2012; Nixdorf and Boehrer 2015). Boehrer and Schultze (2008) refer to the importance of evaluating all processes that are known from scientific literature for sustaining meromixis, since several processes may be acting simultaneously. Here we explain the important processes that can sustain meromixis and support each of these processes by the clearest representations we know of in the environment.

To provide a better overview, we list all the processes that have been documented to form and sustain meromixis, before we go into the details and mention the representative examples from the literature. We mainly see a distinction into two groups: those which operate purely mechanically (where we include salt exclusion at ice formation) and those at which geochemistry of lake waters takes the control. Though we treat the geochemistry as a set of chemical reactions, many of

these processes are mediated by organisms. For details, we refer to the subsequent sections and chapters of this book.

1. Purely mechanical:

- (a) Salty inflows into lakes:
 - From external sources
 - From groundwater
- (b) Freshwater onto salty lakes:
 - From external sources
 - Salt exclusion at ice formation
- (c) Partial deepwater renewal:
 - Evaporation in side bays
 - Cooling in side bays
 - Salty intrusions from ice

2. Involving geochemistry:

- (a) Decomposition of organic material
- (b) Iron meromixis
- (c) Temperature-dependent solubility of mirabilite
- (d) Calcite precipitation

The local distribution of these mixing and stratifying processes is shown in a schematic display of a lake (Fig. 2.4).

Salty inflows that find their way to the deep layers of a lake can form a permanent stratification, no matter whether these inflows enter at the surface of lakes (Lake Nitinat, Canada: Ozretich 1975) or as groundwater (see Fig. 2.4; Kongressvatn, Norway: Bøyum and Kjensmo 1970; Wallendorfer See and Rassnitzer See, Germany: Böhrer et al. 1998; Heidenreich et al. 1999; Waldsee, Germany: von Rohden et al. 2009, 2010; see also Chaps. 6 and 12 for more

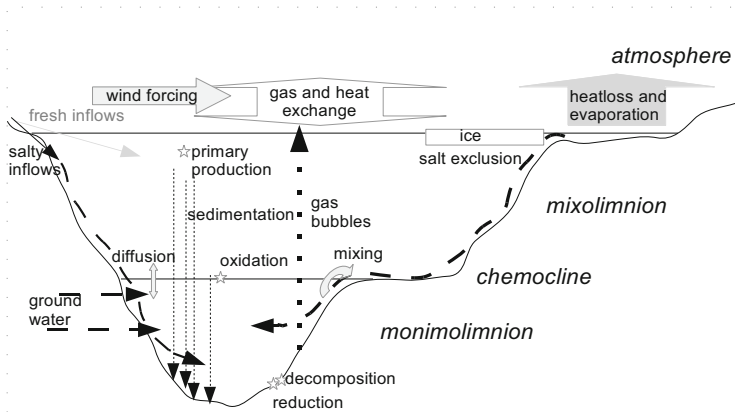


Fig. 2.4 Sketch of processes involved in sustaining meromixis

examples). Sibert et al. (2015) reported meromixis caused by salty wastes entering the lakes and formed by salt used for de-icing of roads; Scharf and Oehms (1992) also reported the same for meromixis in Lake Schalkenmehrener Maar (Germany). High-salinity water can also be produced in the lake itself by enhanced evaporation in a shallow side bay, as in the Dead Sea in the period before 1979 (Nissenbaum 1969). Because only a small portion of the monimolimnion is replaced, the monimolimnion chemistry (e.g., oxygen concentration) is not greatly affected. Salt exclusion during ice formation can also act as a source of saline water (Antarctic lakes: Kerry et al. 1977; Gibson 1999).

In addition, density stratification in the mixolimnion is reinforced when less saline ice melts in spring and forms a water layer of reduced density near the surface, which needs to be removed before turbulent kinetic energy can effectively erode the density stratification at the upper edge of the monimolimnion (e.g., Lake Shira, Russia, Chap. 5). Snowmelt in the vicinity of meromictic lakes and freshwater runoff from snowmelt add to the effect of melting lake ice (e.g., Hammer 1994; Zachara et al. 2016). During wet season, high runoff may also support meromixis by bridging the density stratification into the thermal stratification period especially in regions where precipitation occurs almost exclusively seasonally (e.g., Santofimia et al. 2012). They also reported a full overturn when the precipitation came too late in the year to accomplish the bridging. High precipitation and consequently higher freshwater inflows have stopped some lakes from circulating for several years (e.g., Lake Mono, USA, see Chap. 11; Jellison and Melack 1993; Jellison et al. 1998; Caspian Sea: Peeters et al. 2000; Lake Van, Turkey: Kaden et al. 2010). Similarly, meromictic lakes were formed where fjords have been disconnected from the ocean by land rising after glaciers had receded at the end of the ice age, e.g., Rørdholtfjorden, Norway (Strøm 1957); Powell Lake, Canada (Williams et al. 1961); and lakes in coastal regions in the northern Baltic Sea (Lindholm 1996). Some of these lakes maintained their stratification for several thousand years. Seawater was capped with freshwater to create a meromictic lake in the former Island Copper Mine (Canada; see Chap. 9). Controlled freshwater input in lakes Wallendorf and Rassnitz (west of Leipzig, Germany) was used to quantify the effect of shielding the deepwater stratification by a freshwater introduction (Boehrer et al. 2014).

In principle, density-driven flows as described above can also be caused by temperature differences. However, density difference due to temperature is limited to 2 kg/m or 3 kg/m, while density differences due to solute concentration can be one to two orders of magnitude higher. In addition, molecular diffusion of heat is faster (factor ~100) than diffusion of solutes, and hence a density stratification due to temperature is more affected by diffusion. Thus, meromictic lakes due to temperature-driven flows are rare. Similarly, Dead Sea (before 1979), where evaporation created saltier and hence denser water in the south basin, is a good example of creation of meromixis: also surface cooling during southern winter at the south end of Lake Malawi/Nyasa (Malawi, Tanzania, Mozambique) produces sufficiently dense water to intrude the monimolimnion (Vollmer et al. 2002a). Lakes with partial deepwater renewal are called meromictic, only if a sufficient portion of

the monimolimnion is replaced to sustain the stratification, but not enough to make dissolved oxygen to be detectable in the monimolimnion.

In addition to water currents, solute precipitation can effectively transport matter through the water column. If salts of high sodium and sulfate concentration are excluded from the ice formation, mirabilite ($\text{Na}_2\text{SO}_4 \cdot 10\text{H}_2\text{O}$) may precipitate. Hammer (1994) reports such precipitation below the ice at temperature close to 0°C for Waldsea Lake (Canada). The settling mirabilite removes solutes—and hence their density contribution—from the cold surface water, but it gets redissolved in the monimolimnion due to the higher temperatures ($5\text{--}7^\circ\text{C}$; Hammer and Haynes 1978) and the strong dependence of mirabilite solubility on temperature (Marion and Farren 1999; see also Chap. 3). The density contribution is added to the monimolimnetic waters. The picture gets slightly more complex when biogenic calcite formation accompanies photosynthesis. With increasing photosynthetic activity, pH increases such that carbonate will form from dissolved bicarbonate in the epilimnion. Eventually the solubility product of calcite is exceeded, and calcite precipitates and sinks to deeper layers. High CO_2 partial pressure in the monimolimnion, e.g., from decomposed organic material, allows a redissolution of calcite (Lake La Cruz, Spain: Rodrigo et al. 2001; see also Chap. 8). Also in this case, the calcite removes the density contribution of solutes from the mixolimnetic waters and adds it to monimolimnetic waters.

Waldsea Lake (Canada) and Lake La Cruz (Spain) demonstrate that reactivity of solutes can inhibit the deep recirculation, but only, if this process transports solutes up the gradients, which means from low concentrations in the mixolimnion to high concentrations in the monimolimnion, effectively enough to compensate for the diffusive and turbulent transport down-gradient. This is facilitated by limited solubility of a substance: particulate solids are formed and precipitate and sink down to the monimolimnion. If conditions in the monimolimnion are favorable, these precipitates can redissolve at least in part. To keep this chemical cycling of matter going, an energy source must be accessible. In nearly all cases, energy is provided by organic material, which has gained its energy from photosynthesis, and feeds it into the chemical cycle on being decomposed. Organisms usually have a slightly higher density than water, and hence they settle to the lake bottom still alive or after they die. Organic material can be oxidized by microorganism, releasing CO_2 , which contributes effectively to water density. The oxidizing agent in this process is important, as the net effect of released products must yield a considerable increase in density. Both oxygen (classic biogenic meromixis) and iron (iron meromixis) are good oxidizing agents to raise density sufficiently in the monimolimnion. Also other oxidizing agents (nitrate or sulfate) may be present, but they have not yet been demonstrated to be the primary factor for building the density gradient needed for meromixis.

Iron is present in many mine lakes but also in natural lakes originating from the soil and rocks in the catchments. However, if dissolved oxygen is present in the mixolimnion and if in the upper part of the chemocline, iron gets oxidized to ferric iron Fe(III) , it precipitates as hydroxide in water at pH above 3.5 (e.g., Stumm and Morgan 1996). On the contrary, in a monimolimnion where no dissolved oxygen is