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Carbon uptake in lakes

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Summary

The fate of radiocarbon (14-C) originating from a geological repository of radioactive waste is a key question when estimating the potential dose to humans and environmental impacts. This report presents the different biotic and abiotic processes related to uptake and release of mineral carbon (CO_2 and CH_4) and movements of the mineral and organic carbon between different carbon pools and lake compartments (epilimnion, metalimnion, hypolimnion). The focus is put on small lakes with high inputs of organic matter from the surrounding catchment area and the pelagic parts of these lakes.

Carbon fluxes between different pools (e.g., from organic to inorganic) as well as from one lake compartment to the next (e.g., from the hypolimnion to the metalimnion, or from epilimnion to the atmosphere) vary significantly in time and space. Climate related processes, such as lake mixing or heavy rain, often lead to rapid losses of inorganic carbon forms (gasses), while biotic processes are more stable over time but depending on the conditions may be slow (eg. oxidation of methane in low oxygen environments). Especially important are processes that may change the proportions between 14-C and 12-C, such as carbon flow from the atmosphere or the catchment to the lake, as these may dilute the 14-C concentration in the water column.

Important for the dose to humans is to acknowledge the flow of carbon up in the food web as carbon from both, CO_2 and CH_4, has been demonstrated to be transferred even to fish. Also, it is important to acknowledge that most lake processes are depending on the lake conditions defined by climate and, thus, may change in the future together with the changing climate.

Sammanfattning

Ödet för radioaktivt kol (14-C) är avgörande för att kunna göra riskbedömningar förknippade med utsläpp av radioaktivitet från ett geologiskt slutförvar. Denna rapport presenterar biotiska och abiotiska processer som påverkar upptag och frisättning av oorganisktkol (CO_2 och CH_4), och flöden av organiskt och oorgansikt kol mellan olika kolförråd och mellan olika vattenmassor av en sjö (epilimnion, metalimnion, hypolimnion). Fokus ligger på små sjöar, som påverkas starkt av mängden organiskt material från avrinningsområdet, och berör främst de pelagiska delarna av dessa sjöar.

Flöden mellan olika förråd av kol (t.ex. från organisk till oorganisk form) eller mellan delar av sjön och dess omgivning (t.ex. från hypolimnion till metalimnion, eller från epilimnion till atmosfären) varierar i hög grad i tid och rum. Klimatrelaterade processer, som vattenomblandning och kraftiga regn, leder ofta till snabba förluster av oorganiskt kol (gaser). Biotiska processer är mer stabila över tiden men kan de vara långsamma beroende på förhållandena i sjön (t.ex. oxidation av metan i miljöer med låg syrehalt).

Processer som kan ändra proportionerna mellan 14-C och 12-C är särskilt viktiga för bedömningar av säkerhet, eftersom stabilt kol kan späda ut 14-C-koncentrationen i vattenpelaren. Exempel på processer som kan leda till utspädning är flöden av stabilt kol från atmosfären, eller från avrinningsområdet, till sjön. Radioaktivt kol transporteras även upp genom näringsväven, och C-14 från både CO_2 och CH_4, återfinns i fisk, vilken i sin tur kan konsumeras och ge dos till människa. De flesta processerna är beroende av förhållandena i sjön, som i sin tur styrs av klimatet. Detta innebär att process-hastigheter sannolikt kommer att förändras i takt med klimatförändringar.

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1 Introduction

Disposal of radioactive waste comes with many challenges. The preferred solution is to isolate this hazardous waste from the living environment, until the activity is low enough to not represent a risk to life (e.g., IAEA 1997, ICRP 2013). The task of the Swedish Nuclear Fuel and Waste Management Company, is to deal with all the radioactive waste from nuclear power plants in Sweden in a safe way. The selected solution will be to dispose the waste in deep bedrock (e.g., SKB 2015, 2017, 2020). This is not only a legal obligation as stipulated by the Swedish regulations (SSM 2009) but also a moral and ethical necessity for our generation. The key aspect of this review is to provide the scientific background needed to adequately represent the uptake of radio carbon in aquatic environments in the radiological risk assessments for humans and the environment.

1.1 Focus of the present report

This report focuses on the specific risk associated with potential leaks of 14-C gas (i.e., $^{14}CO_2$ and $^{14}CH_4$) into lakes. With the low- and intermediate-level waste, 14-C constitutes a considerable part of the potential radiological risk. The chemical forms of 14-C compounds bound in the waste are poorly known, but the presence of microbial life means that any organic compound can potentially be turned into CO_2 through respiration or fermentation. Furthermore, the conditions expected to prevail in the repository (no oxygen and H_2 availability as a by-product of canister oxidation) could lead to microbial production of CH_4. As gas moves upward driven by strong buoyance forces, they might reach the biosphere. This report aims to describe the potential fates of $^{14}CO_2$ and $^{14}CH_4$ molecules that would enter the biosphere through lakes. In the scenario considered, the radioactive carbon would seep through the bedrock to the sediment and the water column of a lake. This report mostly focuses on 14-C path in the pelagic water, that is, the area of a lake where no vegetation grows attached to the lakebed. However, benthic primary production can be important in shallow lakes and will therefore be considered in a specific section (see Chapter 7). More information on the benthic and littoral environments, sediment processes and gas fluxes between the water column and atmosphere can be found in SKB R-21-20 (Ikonen 2021).

Furthermore, this report does not consider the fate of 14-C reaching the biosphere in other parts of the watersheds of hypothetical lakes. Any 14-C that would reach the biosphere can potentially be incorporated into organic matter. This organic matter can then be washed away and carried to lakes by surface runoff, ground water and rivers. One critical aspect for risk assessment is the potential accumulation of 14-C along the food chain. As the concentration of 14-C in potentially edible organisms depends strongly on the ratio of 14-C/12-C in the water (see Section 5.3), understanding how these ratios can vary within the different compartment of a lake is of importance.

Overall, this report aims to give the reader key understanding on what are the possible fates for 14-C reaching a lake. It will therefore quickly introduce lake functioning and then present the different metabolic and physical process which can affect 14-C fate in lakes. Based on these processes it will finally present the different ways 14-C could leave the lakes or be trapped in the lakes for longer period of time and potentially accumulate.

1.2 Lakes – structures and dynamic

1.2.1 Lake typology based on the physics

Lakes are inherently heterogenous and their physical, chemical, and biological characteristics vary even within a lake. This heterogeneity is both spatial and temporal and can be driven by a variety of variables including, but not limited to, wind, solar radiation, topology, currents, and temperature. The scale of the variation within a lake can vary from micrometers to kilometers and from minutes to geological time scales. For the sake of clarity this report will focus on scales that are the most relevant to predict the fate of volatile 14-C reaching a lake. Even though it is unnecessary to consider every microvariation affecting lakes, it would be misleading to consider lakes as homogenous bodies of water. The variation most important and relevant for carbon uptake is stratification.

Stratification is the natural tendency of a lake to form separate and distinct layers of water. The primary driver of stratification in lakes is heat. As the top layer, exposed to sunlight, warms up, it becomes less dense and floats over colder, denser water. This creates three distinct layers. A top warm and light layer, called epilimnion, a cold and denser layer at the bottom (the hypolimnion) and finally an intermediate but distinct layer: the metalimnion. Depending on the lake area, depth, vertical shape, and exposure to wind the stratification can last from days (polymictic lake) to centuries (meromictic lakes). In a boreal context most lakes mix at least once a year as the decreasing temperature in the autumn allows the top layer to sink and facilitates mixing while also wind and precipitation increase. Whereas it is common to see lakes mixing a second time in the spring, this is not systematic in the boreal landscape. Indeed, the dark color often observed in boreal lakes favorizes a quick heating of the top layer soon after the ice off, limiting the chance of a spring mixing. The mixing pattern of lakes is important for predicting the fate of 14-C seeping into lakes. Low temperature and high pressure allow CH_4 and CO_2 to accumulate in the hypolimnion. Whereas low solubility of CH_4 limits this accumulation (see Chapter 6), this is not the case for CO_2 that instead can be released massively during mixing or other sudden degassing event.

Once the thermal stratification is set, the hypolimnion is isolated from the epilimnion and atmosphere. This can lead to a chemical stratification generally led by the absence of oxygen replenishment. Oxygen can also be provided by photosynthetic organisms, but often the hypolimnion does not receive enough light for oxygenic photosynthesis (see Sections 2.3 and 2.4). As microorganisms consume oxygen, the hypolimnion becomes poorly oxygenated and in certain cases totally depleted. This later case can occur when stratification lasts for a longer period or if the water is rich in organic matter, increasing microbial respiration. At the interface between the oxic epilimnion and the anoxic hypolimnion a steep and stable gradient of oxygen, salinity and redox couples is generally observed (Børsheim et al. 1985, Camacho et al. 2001). The depth at which this gradient is observed is named the chemocline, and it overlaps with the metalimnion.

Most lakes develop thermal stratification during the summer, but their hypolimnion does not necessarily become anoxic. For instance, in clear oligotrophic lakes oxygen consumption is low and oxygenic phototrophs maintain oxic conditions below the thermocline (Nürnberg and Shaw 1998). On the other hand, small colored lakes are more likely to possess an anoxic hypolimnion (Nürnberg and Shaw 1998) even when very shallow. This is the result of the combination of limited oxygenic photosynthesis due to lower light penetration and higher heterotrophic respiration due to high organic carbon concentration. The presence of oxygen stratification is particularly important as it plays an important role in the biological filter for both CO_2 and CH_4 originating from the hypolimnion and sediment.

With climate change, shorter ice-covered periods and higher summer temperatures have been observed. Both phenomena have an impact on the stratification regime of boreal lakes. First, warmer temperature and earlier ice off might lead to a longer period of stratification, and in case of absence of ice, potentially to several years without complete mixing. Second, longer summers and an increase in precipitation are expected to have an impact on the plant production in the watershed, leading to higher organic matter discharges to lakes. This process has the potential to reinforce thermal stratification by increasing the coloration of water (browning), but also to accelerate oxygen depletion by limiting oxygenic photosynthesis and increasing heterotrophic respiration.

1.2.2 Lake typology based on their chemistry

The report "The limnic ecosystems at Forsmark and Laxemar-Simpevarp" from Eva Andersson (Andersson 2010) offers a detailed presentation of lakes relevant in the context of the nuclear waste disposal facilities in Sweden. It also gives a short introduction to what is a lake. The definition of what qualifies as a lake differs in the literature, but it generally refers to a body of freshwater where the water is retained (as opposition to a stream). In the case of Andersson´s report the definition used is "a body of freshwater with a minimum size of 0.5 ha surrounded entirely by land".

The chemical composition of a lake is largely a function of its climatic zone, which affects the hydrology of the watershed, and its basin geology. Lakes with high concentrations of calcium (Ca^{2+}) and magnesium (Mg^{2+}) are called hardwater lakes, while those with low concentrations of these ions are called soft water lakes. The first ones are associated with calcareous bedrock, like found in the Forsmark area, whereas the latter are found in areas where the bedrock is granitic, like in the Laxemar-Simpevarp region. This difference is particularly relevant as high concentrations of calcium ions (Ca^{2+}) lead to higher pH and precipitation of carbonates (see Section 6.4).

Some other ions also play an important role in the lake chemistry, particularly phosphate, nitrate, and ammonium. Phosphate can be of geological origin, while nitrogen ions are products of biotic processes. The concentrations of these three ions are also strongly influenced by human activities, particularly by fertilizer runoff and wastewaters. Lakes with high phosphorus and nitrogen concentrations are called eutrophic, whereas lakes with low concentration of these elements are called oligotrophic.

Lake organisms play a major role in lake chemistry. Living organisms can modify lake chemistry by producing, degrading or modifying organic compounds. They also strongly affect the chemistry of mineral ions. This effect can be direct, like when organisms directly consume these compounds, organic or mineral, for energy generation or assimilation in their biomass, or indirect by modifying the environment. Examples of these changes in the environment are pH modification, shading and coloration that can impact the temperature and light penetration, and modification of the redox conditions. Living and dead organisms also influence lake chemistry and physics by offering nucleation sites for precipitation of minerals and organic compounds.

1.3 Carbon cycle

Lakes are hotspot for carbon cycling. In its simplest form the carbon cycle could be described as a reversible reaction of CO_2 with water into organic compounds. In one direction energy is needed to reduce CO_2 to an organic compound, and in the other direction energy is released as organic molecules are oxidized to produce inorganic C, i.e., CO_2. A similar cycle exists for CH_4, but some major differences exist, one being that whereas CO_2 fixation requires an external source of energy, in both production and oxidation of methane the carbon source is also the energy source (see Chapter 3).

Also, one could argue that CH_4 is organic in nature. But for the sake of simplicity, it is in this report considered as a form of inorganic C. As this choice is strictly semantic in nature, this has no impact on the analysis of carbon uptake in lakes, but allows the inclusion of both CO_2 and CH_4 in a common category of inorganic C. It is now possible to define carbon uptake as the incorporation of inorganic carbon into biomass. Biomass can be transferred to higher trophic levels, including humans, accumulate in the sediments, or be exported downstream. Both CO_2 and CH_4 can exit the aquatic system as gas to the atmosphere. Besides, depending on the lake chemistry, part of the CO_2 can precipitate as carbonate minerals (see Section 6.4).

The simplicity of the C cycle presented above is of course far from reality. The path of carbon-based molecules in lakes are not linear. Each 14-C atom of CH_4 or CO_2 transformed or incorporated into biomass has a chance to be recycled to a mineral C form or transformed into a variety of other C-based compounds. These compounds can be very stable with a residence time in the environment up to geological scale. But some other compounds will be consumed rapidly by microbes or organism on a higher trophic level. Part of this C will be incorporated into the biomass of upper trophic levels, whereas some will be released as CO_2 or CH_4, depending on the organism. That newly released inorganic C can then be incorporated again or exits the system to the atmosphere.

The next sections will explore the different mechanisms that are likely to favorize 14-C release to the atmosphere or, on the contrary, to increase the chance of 14-C being accumulated in the food chain and/or in the sediment. Chapters 2 and 4 will describe the biological processes responsible for the transformation of mineral carbon to carbohydrates and vice et versa, whereas Chapter 3 will focus on the specific case of the methane cycle. The different mechanisms with a potential to trap and accumulate 14-C in lakes will be assessed in Sections 5.3 and 5.4. Finally, Chapter 6 dwells on mineral carbon pools that are likely to evade the lake to the atmosphere as well as the pathways associated with them.

2 CO_2 immobilization processes

In this section we explore the carbon pools, chemical reactions and biological pathways that might lead to $^{14}CO_2$ immobilization and/or accumulation in lakes. In the absence of life, the fate of $^{14}CO_2$ leaking from the repository would only be dictated by their solubility and transport rates. But as life is a key component of lakes the fate of $^{14}CO_2$ depends strongly on biological pathways. In this section we explore the different biological pathways that can transform CO_2 into organic matter, and thus, potentially trap 14-C into biomass.

2.1 Photosynthesis

Photosynthesis is a biological process which allows the transformation of CO_2 into complex organic compounds and the conversion of solar energy into chemical energy. Photosynthesis is the base of all humanity's food and oxygen sources and its fossilized product provides more than 80 % of the world's energy (Johnson 2016). Photosynthesis can be performed by plants, algae, and bacteria. In the context of this report, we will focus on the production of algae and bacteria. Photosynthesis can be split in two groups of metabolisms. One is oxygenic photosynthesis, in which the electron source for CO_2 reduction comes from water. In that case, as suggested by the name oxygenic, O_2 is a byproduct of the reaction alongside hydrocarbons. This is the photosynthesis performed by plants, algae, and cyanobacteria. Alternatively, some photosynthetic bacteria are unable to oxidize water and use alternative electron sources like sulfide, molecular hydrogen, ferrous iron, or arsenic. The first clear understanding of the redox nature of photosynthesis came as Van Niel was studying such sulfur reducing phototrophs (Niel 1932). He proposed a general equation for photosynthesis. This general reaction of photosynthesis is

$$2H_2A + CO_2 \rightarrow 2A + CH_2O + H_2O$$

where H_2A is the reductant and A is the oxidized product. The better-known reaction for oxygenic photosynthesis is a special case of the previous equation:

$$6CO_2 + 6H_2O + \text{light} \rightarrow C_6H_{12}O_6 + 6O_2$$

2.2 Oxygenic photosynthesis

Oxygenic photosynthesis in lakes is performed by plants, macroalgae, a diverse group of organisms generally referred to as phytoplankton, as well as benthic microphytes.

Plants, macroalgae and benthic microphytes are associated with shallow benthic environments, which means they develop attached to the bottom of lakes where light is available, whereas phytoplankton live suspended in the water column. Both phytoplankton and benthic microphytes include both eukaryotes (microalgae) and prokaryotes (cyanobacteria). Algae is a poorly defined polyphyletic taxonomic group which includes aquatic photosynthetic organisms that lack stem, roots, and leaves. Whereas estimate of the algal diversity range from 30'000 up to over a million, 15 phyla and 54 classes were recorded in the reference database as of 2012 (Guiry 2012). It includes macroscopic organism like kelp as well as microorganism, both mono and pluricellular. Unlike algae, all cyanobacteria belong to a very diverse but monophyletic group. This lineage is globally responsible for much of the primary productivity and nitrogen fixation and is present in a wide variety of habitats. It is also generally accepted that their photosynthetic activity provided much of the oxygen leading for the proliferation of aerobic life (Dvořák et al. 2017).

The equation for oxic photosynthesis presented above, while correct, hides the complexity of the process it describes. Photosynthesis encompasses a large number of reactions some of which remain to be elucidated. Interestingly all oxygenic photosynthetic organisms use the same process. This common chemistry is explained by the widely accepted hypothesis that chloroplast, the site of photosynthesis in all eukaryotic phototroph (plants and algae), evolved from an symbiotic relationship of a prokaryote with a cyanobacterium (Turner 1997). In short, oxygenic photosynthesis can be divided into two phases. The first, generally referred to as the light-dependent reaction, consists of the absorption of light by a pigment (i.e., chlorophyll) and the subsequent transfer of the excitation energy to the reaction centers (Photosystems I and II). Photosystems I and II use that energy to respectively generate reducing equivalents (i.e., NADPH) and to split H_2O. They additionally create a transmembrane proton gradient which allows the production of ATP, the "energy currency" of cell biochemistry. The second phase, referred to as light-independent or dark reaction, includes the conversion of CO_2 into carbohydrates using the ATP and reducing power (NADPH) provided by the light-dependent part of the process. This conversion happens via the Calvin–Benson–Bassham cycle and the enzyme Rubisco. Rubisco is considered as the most abundant protein on earth as all oxygenic photosynthetic organisms use it to fix carbon. The metabolic differences between cyanobacteria and algae (or plants) driven photosynthesis are minor. The main differences are minor variation in the structure of their chlorophyll and the cell location of the described processes. Despite the variation in chlorophyll results in slightly different absorption spectra, they all absorb light mainly in blue and red regions of the visible spectrum (Jagannathan and Golbeck 2009).

Photosynthesis is an efficient process, and it has a potential to consume all available CO_2. This ability is what makes ocean a carbon sink (Wanninkhof et al. 2013). For lakes, models suggest that lakes with DOC concentrations near zero would have pCO_2 near zero, which is incompatible with physical principles of gas dissolution (Larsen et al. 2011). This suggests that phototrophic organisms in lakes have a potential for C fixation higher than the flow of CO_2 from the atmosphere to a lake. Similarly a full lake 14-C incubation experiment showed that in eutrophic conditions phytoplankton can consume almost all available mineral C (Bower and McCorkle 1980, Stephenson et al. 1995). But if photosynthesis rates are generally limited by light as well as P and N availability (Hecky and Kilham 1988, Ogbebo et al. 2009), recent work suggests that dissolved inorganic carbon availability might play a role in primary production rates (Kragh and Sand-Jensen 2018). In this study nutrient rich water with high pH led to increased primary production rates. Kragh and Sand-Jensen (2018) suggest that high DIC supported phytoplankton productivity by direct algal uptake of bicarbonate, through the release of CO_2 coupled to calcification and by inducing high pH that greatly enhances atmospheric CO_2 invasion. However, despite the efficiency of phytoplankton in fixing CO_2, it is generally accepted that most lakes are oversaturated in CO_2 (Cole et al. 1994, Raymond et al. 2013). Although the source of that CO_2 is still discussed, it is clear that the mineralization of allochthonous organic carbon and lateral inorganic carbon fluxes are important sources of CO_2 in lakes (Weyhenmeyer et al. 2015). In any case, $^{14}CO_2$ reaching the photic zone of the lake will be mixed with CO_2 from other sources, leading to a dilution of radioactive CO_2. Whereas lakes are generally considered as net emitters of CO_2, this is not true for all lake. The role of small lakes (ponds) as sources or sinks of carbon is still controversial (Taylor et al. 2019, Goeckner et al. 2022) and clear lakes with low DOC may act as sinks. That appears to be particularly true for clear shallow lakes where benthic macroalgae and photosynthetic microbial mats are responsible for most of the primary production (Andersson 2010, Ask 2010).

2.3 Anoxygenic photosynthesis

Anoxygenic photosynthesis, as its name suggest, does not produce oxygen. This comes from the fact that the diverse alternative electron donors (e.g., S^0, H_2S, Fe^{2+}, H_2) do not contain oxygen. Although the overall process has some similarity with oxygenic photosynthesis, the metabolism of anoxygenic photosynthetic bacteria differs in several aspects from what is observed in Cyanobacteria and eukaryotes. As in oxygenic photosynthesis, light energy is captured to facilitate an electron transfer, that is then used to synthesize ATP via the generation of a proton gradient. The electrons are also used to produce reducing power necessary for CO_2 fixation. Besides the electron donors, there are a few main differences. First, the light capturing pigment in anoxygenic photosynthesis belongs to a different family of molecules called bacteriochlorophyll. They are similar to chlorophyll, but absorb light in a different range of wavelength. Critically, their ability to capture light in the near infrared allows them to be effective in very low light environment, Second, the reducing equivalent is NADH rather than NADPH. Third, they only use one photosystem. Some use photosystem I whereas others use photosystem II. Finally, while some anoxygenic photosynthetic bacteria use the Calvin cycle, the light-independent part relies on a diversity of metabolisms depending on the organism. Beside the metabolic difference in the photosynthesis, anoxygenic photosynthetic bacteria generally live in anoxic environment and have a very low tolerance for oxygen[1].

Anoxic photosynthetic bacteria have been detected in several boreal lakes and might represent an important part of the microbial population of the anoxic water column (Karhunen et al. 2013, Tsuji et al. 2020). However, their contribution to carbon fixation rate is hard to assess as they generally are active in the same depth as chemolithoautotrophs, which also fix CO_2 (next section). The total carbon fixation by chemolithotrophs and anoxygenic phototrophs represented 50 % of the total primary production in at least two different lakes (Kuuppo-Leinikki and Salonen 1992, Camacho et al. 2001, Storelli et al. 2013), and in one case in Israel even 80 % (Thompson et al. 1990). However, it is unclear how representative those results are for lakes in general, and especially those with very light water colour. The importance of anoxygenic and dark carbon fixation varies from lake to lake, and probably also seasonally, but might be particularly important in humic boreal lakes due to their low light levels and stratification (Kuuppo-Leinikki and Salonen 1992, Martin 2021).

2.4 Chemolithoautotrophs

Chemolithoautotrophy is the ability of some prokaryotic organisms (bacteria or archaea) to fix inorganic carbon into organic matter without the use of solar energy. Chemolithoautotrophs get the energy and reducing power necessary to turn CO_2 into carbohydrates from the exergonic oxidation of reduced compounds. Chemolithoautotrophs are a diverse taxonomic and metabolic group. Similarly, there are numerous pairs of oxidized and reduced compounds with a potential to provide the energy for C fixation. Some steps of the methane cycle can be considered as chemolithoautotrophic in nature (e.g. CO_2 reduction to CH_4, and CH_4 assimilation). These will be treated in detail in the section about the methane cycle (see Chapter 3).

The importance of chemolithoautotrophy in aquatic ecosystem varies, but several studies suggest that it can fix as much carbon as photosynthesis (Camacho et al. 2001, Nõges and Kangro 2005). However, the importance of dark carbon fixation is expected to vary with lake chemistry and seasonal changes in the stratification status of the lakes. In some instances no dark fixation could be detected in the chemocline of a freshly stratified boreal lake (Martin 2021) and dark fixation varied widely from lake to lake in a survey of dark carbon fixation in northern Spain. Based on short term in situ incubations in five different lakes, 4 % to 31 % of the total carbon fixation was due to dark carbon fixation (Casamayor et al. 2012). It was also recently demonstrated that chemolithoautotrophy is widely spread in boreal lakes (Martin 2021). The same study suggests that reduction of iron may be the source of energy and reducing power for chemolithoautotrophs in boreal lakes and could therefore mitigate the effect of browning on C fixation in boreal lakes. Indeed, if brownification is expected to reduce light availability it is also expected to increase iron concentration in lakes.

Another important feature of freshwater chemolithoautotrophs is their location in the water column. To gather the energy from redox reactions, they strive where reduced and oxidized compounds coexist. This is generally found at the oxic-anoxic interface, which in lakes is at the chemocline or at the sediment surface if the lake does not have an anoxic hypolimnion. In context of dark stratified boreal lakes dark carbon fixation was also detected in the epilimnion but the faster incorporation rates were measured in the metalimnion and at the top of the hypolimnion where oxygen level was below the detection limit. Based on a study of 18 lakes the daily rate for dark carbon incorporation varied from 0.17 µM to 13.31 µM (Martin 2021).

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[1] For the sake of completeness, it is worth mentioning that also several aerobic anoxygenic phototrophic bacteria have been described. These phototrophs are peculiar as even though they are able to capture light energy, they are unable to fix carbon (Hanada 2016). Their importance in the carbon cycle is not clear, but might be more relevant in very oligotrophic waters. Furthermore, their role in the carbon cycle is as a carbon mineralizer rather than as a carbon fixer.

This is particularly relevant for understanding the fate of $^{14}CO_2$ leaking from the bottom of the lakes to the water column as it will have to cross this chemocline where there is an active community of organism able to turn CO_2 into organic matter. This community includes not only chemolithoautotrophs but also anoxygenic photoautotrophs (see Section 2.3).

2.5 Bloom

Carbon fixation rates have significant spatiotemporal variability. Part of this variation is associated with seasonal changes and stratification. Another case to consider are intense short-term blooms. During phytoplankton blooms typically net heterotrophic lakes can become temporarily net carbon sinks (Yezhova et al. 2021). Despite the potential for C capture, blooms are generally considered as a nuisance as cyanobacterial blooms have a potential to poison water supply and recreational area. Furthermore, when decomposing, blooms can lead to massive hypoxia events leading to fish kills. Factors leading to blooms in lakes are still unclear, but temperature, pH, light conditions, P and N concentrations, oxidative stressors, interactions with other biota (bacteria, viruses and animal grazers), and most likely, the combined effects of these factors, are generally considered as important variables in blooming events (Paerl and Otten 2013, Trigal et al. 2013, Ger et al. 2014, Vuorio et al. 2020). Consequently, increased human land use leading to eutrophication of waters as well as the ongoing climate change are expected to increase the frequency of blooming events (Paerl and Huisman 2008). Beside their potential toxicity, blooms could provide a poor quality food for grazers (Peltomaa et al. 2013). This might explain why, during blooms, sedimentation can represent up to 72 % of the primary production (Lignell et al. 1993). High CO_2 consumption by phytoplankton can also lead to increased pH and carbonate precipitation (Thompson et al. 1990).

Methanotroph (see Section 3.2) blooms have attracted way less attention and very little is known about them. Nevertheless, recent studies suggest that they might exist and play an important role in limiting CH_4 emission from lakes. Indeed, the observations of methanotroph blooms have been associated with lake overturn. Critically, it appears that those blooms can consume most, if not all of the methane accumulated in the hypolimnion during the stratification period (Graf et al. 2018, Mayr et al. 2020a).

3 Methane

When considering the CO_2 side of the carbon cycle things are relatively straightforward. CO_2 can be reduced and incorporated into the organic carbon pool by photosynthetic and chemolithoautotrophs organism. This reduction of CO_2 needs an external source of energy and the substrate is incorporated into the biomass of the organisms. The produced biomass can then be mineralized (i.e., oxidized), which will provide energy and produce CO_2 as a by-product. When methane is considered, things get a bit murkier. Indeed, during both biogenic production and consumption of methane the carbon source is also the energy source. CO_2 reduction with H_2 provides methanogens with a source of carbon, reducing power (electrons) and energy. Similarly, during oxidation of CH_4 by methanotrophs, CH_4 reaction with O_2 provides the carbon source, the reduction power and energy. In this section we will explore the methane cycle, its relationship with the CO_2 cycle and its relevance for predicting the fate of 14-C leaks into a boreal lake.

3.1 Methanogenesis

Methanogenesis is the ability of certain microbes to produces methane. Recent studies have demonstrated that some organisms like cyanobacteria are able to produce methane in oxic conditions (Bižić et al. 2020, Günthel et al. 2020), but traditionally methane production is associated with anoxic conditions and archaea. In the traditional model methanogens are strictly anaerobic archaea and can grow by reducing one-carbon compounds (CO_2, CO), acetate, methylated compounds, and coal to methane. They are classified in three functional groups based on their substrate (Buan 2018, Lyu et al. 2018). Hydrogenotrophic methanogens use CO_2 and reduce it with H_2 to form methane, acetoclastic methanogens split acetate to produce CH_4 and CO_2 and, finally, methylotrophic methanogens use methylated molecules to produce CH_4. Interestingly, all these pathways rely on the same enzyme, methyl-coenzyme M reductase, to produce methane. Furthermore, the synthesis of methane is necessary for them to provide the energy needed for their metabolism (i.e. energy conservation). All known obligate methanogens are strict anaerobic archaea (Buan 2018). This "true" methanogenesis is the most relevant to predict the fate of 14-C leaking into lakes. First, it has the potential to reduce $^{14}CO_2$ and organic carbon sources into $^{14}CH_4$. Methane is poorly soluble and, thus, prone to ebullition, which is a potential escape mechanism for $^{14}CH_4$. Furthermore, the production of CH_4 by methanogens has the potential for $^{14}CH_4$ dilution and it increases the possibility to reach over saturation of CH_4, a necessary condition for ebullition. Hydrogenotrophic methanogens are lithotrophs, they also use CO_2 as a carbon source to build their biomass which could immobilize 14-C in the sediment or anoxic hypolimnion. But as methanogenesis provides only very little usable energy, most of the substrate is turned into CH_4 and only 1–40 % of it is used for growth (Buan 2018). Thus, the transfer of 14-C directly from methanogens and up to the food web is low and more likely to happen via methanotrophs.

If methanogenesis *sensu stricto* is limited to anoxic archaea, it is now accepted that a wide set of other organisms also produce methane, including bacteria, algae, plants and fungi (Liu et al. 2022). Metabolisms producing methane in those non-methanogenesis processes may be attributed to demethylation of methylated compounds or by a light driven reduction of CO_2 to CH_4 by a nitrogenase (Fixen et al. 2016). The demethylation processes involved in CH_4 production are not fully understood and the methane produced can be the result of the degradation of different compounds, depending on the organism (Liu et al. 2022). One possible explanation is that demethylation allows a release of immobilized P in P limited environments (Yao et al. 2016). The light induced nitrogenase pathway is also poorly described and the only observations of this process were made during laboratory manipulation including optimization of nitrogenase to produce methane. The potential environmental relevance of this pathway is however supported by work from Bižić et al. (2020). They demonstrated that cyanobacteria could transform CO_2 into CH_4, and suggested that the process is light-driven.

But overall, the detailed biochemistry and physiological purpose of these pathways is still unclear. It appears that these metabolisms are not relevant for neither carbon fixation nor for energy generation. Therefore, they might not play a direct role in 14-C cycling. Nevertheless, they should not be dismissed. Several publications suggest that they might be responsible for the "methane paradox".

That is, the oversaturation of methane in surface water where conditions should allow its total oxidation by methanotrophs (Repeta et al. 2016, Wang et al. 2017). This production could dilute $^{14}CH_4$, but more critically, it could overestimate the $^{14}CH_4$ flux towards the atmosphere. Indeed, if the flux is based on the difference between the CH_4 leaving the sediment and the CH_4 escaping to the atmosphere, the proportion of benthic CH_4 escaping could be largely overestimated. The CH_4 escaping to the atmosphere would indeed not be of benthic origin, but produced in the epilimnion. The methane paradox is a well-known phenomenon and the potential of methane production in oxic water is now well documented (Tang et al. 2016, Günthel et al. 2020). However, it is still unclear if in situ production of methane in the epilimnion is the main cause of elevated CH_4 concentrations in oxic surface waters. Indeed, while some suggest that methanogenesis in oxic water could be the main CH_4 source in large, deep lakes (Bogard et al. 2014), others argue that the CH_4 detected in oxic waters is explained by the lateral transport of CH_4 from shallow littoral zones (Encinas Fernández et al. 2016).

3.2 Methanotrophy

Methanotrophy is the ability of some microorganism to use the oxidation of methane as a source of energy. Methanotrophy was first described more than a century ago, and it was considered to be restricted to aerobic Proteobacteria. However, discoveries made during the last two decades have extended both the metabolic and taxonomical range of methanotrophs. On one hand methanotrophs belonging to other bacterial phyla as well as archaea were discovered, and on the other hand anaerobic oxidation of methane was described (Guerrero-Cruz et al. 2021). Similarly, while it has long been thought that methanotrophs have an obligate requirement of methane for growth, it is now known that some methanotrophs are metabolically versatile (Hakobyan and Liesack 2020).

Aerobic methane oxidation relies on the enzyme methane monooxygenase. Two forms of the enzyme exist. The soluble form (sMMO) is found in the cytoplasm of bacteria, whereas the particulate form (pMMO) is attached to the cell membrane. Most aerobic methanotrophs have pMMO with a few exceptions like *Methylocella* and *Methyloferula*, which only possess sMMO. The two MMOs are structurally very different. Particulate MMO is a single protein comprising three subunits, relies on copper co-factors and is unstable outside the lipid bilayer. Soluble MMO is a protein complex composed of three distinct proteins relying on diiron and is easier to isolate. Despite these differences they both catalyze the same reaction. They oxidize methane to methanol. Subsequently, a methanol dehydrogenase further oxidizes methanol to formaldehyde. Formaldehyde can then be oxidized to CO_2 to gather energy or directed to biosynthesis pathways. By-products of the synthesis (e.g. fructose) can be used for growth or energy conservation depending on the needs of the cell (Bodelier et al. 2019). Alternatively, methanol and formaldehyde can be released or accumulated in the cell when conditions are unfavorable, like when the CH_4/O_2 ratio is low (Harwood and Pirt 1972, Costa et al. 2001). Similarly, some methanotrophs are known to produce high amounts of exopolysaccharides (EPS) when O_2 levels are high but N is limiting (Malashenko et al. 2001, Khadem et al. 2012).

Aerobic methanotrophs are known to strive at oxic-anoxic interfaces, where both methane produced in the anoxic environment is abundant and oxygen is widely available. However, aerobic methanotrophs are also active in the high oxygen low methane epilimnion and in the anoxic hypolimnion or sediment (Rissanen et al. 2018, Reis et al. 2020). Contrarily to the fast growing Gammaproteobacteria dominating the metalimnion, the methanotrophs in oxic epilimnion are dominated by Alphaproteobacteria, which seem to have a high affinity for methane (Martin et al. 2021). High affinity for a substrate allows bacteria to efficiently collect a substrate with low concentration.

The presence and activity of aerobic methanotrophs in anoxic environments are well documented, but the metabolisms involved are still unclear (Guerrero-Cruz et al. 2021). It seems very likely that there is a combination of microaerobic and anoxic process rather than strictly anaerobic. Options suggested are association with photosynthetic (micro)algae serving as oxygen source, use of alternative electron acceptors for the energy conservation or use of fermentation pathway to harness energy from formaldehydes (Guerrero-Cruz et al. 2021). In all these cases oxidation of methane still relies on MMO and therefor on O_2. If the little O_2 available is used for oxidation of CH_4 to methanol, the bacteria must rely on lower energy output pathways like fermentation, potentially loosing methanol or other fermentation by-products (e.g., acetate, lactate, succinate) to the environment (Guerrero-Cruz et al. 2021).

Besides micro-aerobic methanotrophs using alternative energy conservation pathways to live in very low oxygen conditions, non-oxygen dependent, anaerobic methanotrophs have been described. These methanotrophs do not rely on MMO enzyme, but oxidize methane by reversing the last step from methanogenesis. These metabolisms are present in several archaea. These anaerobic methanotrophic archaea (ANME) can use several electron acceptors like iron, manganese, sulfate, nitrate ($NO3^-$) and humic substances. Anaerobic oxidation was also discovered in some bacteria. The bacterium from the NC10 phylum, "*Candidatus Methylomirabilis oxyfera*" is strictly anaerobic methanotroph able to perform "classic" methane oxidation using pMMO. *Methylomirabilis* is getting the O necessary for methane reduction to methanol and formaldehyde via the transmutation of nitrite (NO_2^-) (Wu et al. 2011, Ettwig et al. 2012).

It is generally accepted that methane oxidizers (methanotrophs) consume between 30 and 99 % of the methane originating from the sediments or produced in the water column before it reaches the atmosphere (Bastviken et al. 2008). However, many studies suggest that the efficiency of the methane filter is generally closer to the upper values of that range (Frenzel et al. 1990, Kankaala et al. 2007b, Bellido et al. 2009, Mayr et al. 2020c). An exception to this could be under ice conditions during the winter (Denfeld et al. 2016; Garcia et al. 2019) as the rates of methane oxidation under the ice are highly variable from lake to lake, and the cause of this variation is still unclear (Sawakuchi et al. 2021). However, during winter the methanotrophs do have the potential to limit the emissions by ebullition (Denfeld et al. 2016, Sawakuchi et al. 2021) as the methane is trapped under the ice. Furthermore, limited methane oxidation during the ice covered period could be compensated by methanotrophic bacterial blooms during lake overturns (Graf et al. 2018, Mayr et al. 2020b).

The methane biofilter is *a priori* inefficient to catch summer ebullition. But studies have shown that ebullition was negligible in boreal lakes deeper that 3–6 m (DelSontro et al. 2016, West et al. 2016). It is not clear if this is due to low ebullition or to the efficiency of the methane filter in the sediment (Bornemann et al. 2016). Furthermore, the potential importance of ebullition might be the result of a few discreet seeps (Walter Anthony et al. 2010). This means that even if ebullition is important for estimating the greenhouse gas emissions from lakes, they might not be relevant for estimating the C^{14} flux from the sediment to the atmosphere.

It is not clear what role anaerobic oxidation plays in the biologic methane filter in lakes, but in ocean it is estimated that up to 80 % of the methane originating from cold methane seeps can be oxidized by sulfate dependent ANME (Boetius and Wenzhöfer 2013). However, this ratio dropped to 20 % when seeps had high fluid flow. Anoxic oxidation of methane was also detected in permanently anoxic and seasonally stratified hypolimnion lakes in Switzerland. In both cases the highest rates of CH_4 oxidation were measured below the redoxcline (Su et al. 2017). Finally, a set of studies based on four Siberian arctic lakes showed that anoxic oxidation of methane can consume 60–100 % of the potential net methane emissions, and that there was no CH_4 exchange between the hypolimnion and the epilimnion (Cabrol et al. 2020, Thalasso et al. 2020). They also suggest that most of the methane emissions from these lakes do not originate from the sediments, but from lateral flow or production in the epilimnion, and, hence, escape the anoxic oxidation.

Overall methanotrophs seem to be particularly efficient in capturing methane, especially when methane concentration is high (Reis et al. 2022). Recent studies even suggest that the methane emissions from boreal lakes could be due to methane produced in the oxic epilimnion rather than methane escaping the methanotroph biofilter (Bižić et al. 2020, Günthel et al. 2020).

As aerobic methanotrophs use methane as both, a source of C and energy, it is important to consider their growth efficiency. The assimilated carbon will be added to the organic pool and can serve carbon and energy for the food web or be stored in the sediment, whereas the CH_4 used for energy will be turned into CO_2. Carbon assimilation rates by methanotrophs vary from lake to lake, depending on the methane, O_2, DOC and community structure. But even when the cell abundance of methanotrophs is low, methanotrophs can represent a significant part of carbon consumption (up to 433 $\mu gC\, L^{-1}\, d^{-1}$), potentially more important than heterotrophic respiration (Reis et al. 2022). Depending on the source, the growth efficiency of methanotrophs ranges from 6 to 80 % (6–77 % (Bastviken et al. 2003), 15–80 % (King et al. 1992), 50–80 % (Leak and Dalton 1986).

The least efficient methanotrophs (with up to 88 % of C turned into CO_2) are found in the Alphaproteobacteria. These methanotrophs are generally found in the upper layer of the lake where they live on low CH_4 concentration. The highest incorporation yields were measured for Gammaproteobacteria, which are typically found in abundance at the oxic-anoxic interface of the water column (Martin et al. 2021). These are the microbes probably responsible for the main biofilter of CH_4 in stratified lakes. Gammaproteobacteria are not only efficient in capturing CH_4, but also an important food source for zooplankton as their growth favorizes big cells over multiplication (Reis et al. 2022). Whereas size is not the only factor influencing grazing pressure, large bacterial cells are more likely to be grazed and, hence, lead to accumulation of CH_4 derived carbon in the food chain (Jürgens and Matz 2002, Kankaala et al. 2007a).

4 CO_2 release processes

Carbon based molecule paths in lakes are not linear. Each 14-C molecule of CH_4 or CO_2 transformed or incorporated in the biomass has a chance to be recycled to a mineral C form or transformed into a variety of C based compounds. These compounds can be very stable with a residence time in the environment up to geological times. But some other compounds will be consumed rapidly by microbes or organisms on a higher trophic level. Part of this C will be incorporated in the biomass of the trophic level (see Chapter 5) whereas some will be released as CO_2 or CH_4, depending on the organism. This chapter explores the processes and organisms that can lead to the liberation of 14-C from the biomass back to CO_2.

4.1 Microbial mineralization

Microbial mineralization includes several microbial processes where microbes turn organic matter into CO_2 to gain the energy necessary for their survival and growth. There is a wide variety of processes used to gather energy out of organic matter oxidation, including oxygen-based respiration, and an array of respirations using alternative electron acceptors like Fe^{3+}, NO_3, sulfur, or SO_4. Furthermore, some organisms rely on fermentation, where the only source of ATP is gained by substrate-level phosphorylation. Respiratory organisms also use substrate-level phosphorylation, but in respiration the "excess of electrons" produced during the phosphorylation are sent to an electron transport chain. This electron transport chain allows to, not only recycle the substrate-level phosphorylation electron acceptor (NAD+), but also to significantly raise the energy yield for each oxidized molecule. In the absence of an electron transport chain fermenters must use the byproducts of substrate-level phosphorylation (typically energy rich pyruvate) as final electron acceptor to recycle NAD+(H). Consequently, many fermentation pathways lead to incomplete oxidation of organic matter. However, the end products of fermentation, secreted into the medium as waste metabolites, can yield sufficient energy for the growth of other microbes, and eventually be oxidized to CO_2 (Jurtshuk 1996). In the absence of oxygen, mineralization is expected to be less efficient and slower (LaRowe and Van Cappellen 2011). Although some empirical studies have measured oxidation rates in the anoxic bottom waters that are only about half of what can be measured in oxic conditions (Yang et al. 2005, Isidorova et al. 2016), some other works suggest that oxidation rates in anoxic waters can be similar to those measured in oxic water (Lee 1992, review by Lau and del Giorgio 2020 and references therein). The difference observed from one study to another could be related with grazing, quality of the OM as well as the time frame considered (Lee 1992, Bastviken et al. 2004b).

Microbial mineralization is relevant for at least two reasons. First, it is the main driver of CO_2 production in lakes. It also returns fixed C to the inorganic pool and in that way potentially allows some $^{14}CO_2$ to escape to the atmosphere. Another key aspect of it is that aerobic respiration is consuming oxygen. It is the only mechanism responsible for oxygen depletion in the water column and therefor a key factor in the creation of favorable condition for methanogenesis as well as for all the microbes thriving at the chemocline. This includes methanotrophs, chemolithoautotrophs and anoxygenic phototrophs (see Sections 2.3, 2.4 and 3.2).

5 Fate of immobilized carbon

Immobilized carbon as described in the previous sections can represent a source of carbon for many organisms. When consumed, part of the organic matter will be used to generate energy and be turned back into CO_2 (see Chapter 4) and the rest will be incorporated in the biomass of the consuming organisms. The probability of organic carbon to be consumed depends on availability, degradability, chemical reactivity, and physical properties. In this section we will explore different types of organic matter and how likely it is that this carbon remains immobilized. We will also consider the fates of carbonate precipitates.

5.1 Microbial Biomass

Microbial biomass encompasses the primary producers as well as heterotrophic bacteria. As an important portion of the fixed carbon is lost in solution (exudates), heterotrophic bacteria can capture this organic matter and make it available to upper levels of the food web. In a boreal reservoir, the microbial biomass represented 26.2 to 64.3 % (on average 45.5 %) of the total plankton biomass. Of that microbial biomass, 64 % was composed of heterotrophic bacteria (Kosolapov et al. 2017). The source of the carbon incorporated in the microbial biomass can be CO_2 and CH_4 for primary producers or organic carbon for heterotrophs. Heterotrophic microbes can use a huge variety of carbon sources, which include freshly produced hydrocarbons, that can potentially contain 14-C, if some is available in the environment, as well as allochthonous carbon (see Section 5.2). The microbial biomass varies from lake to lake depending on environmental variables (Zhang et al. 2013) and time, as mentioned previously (see Section 2.5).

5.2 Detrital organic carbon

Detrital organic matter is a term covering all the organic matter that does not belong to a living organism. Detrital organic matter represents up to 99 % of all organic matter in solution or suspension in the water. Detrital organic matter varies in its quality (e.g. chemical composition, function and degradability), size (from dissolved small weight molecules to micrometric particles) and origin (allochthonous vs autochthonous). This section will focus on the last aspect as it is the most relevant regarding the fate of 14-C reaching lake environment.

5.2.1 The autochthonous detrital organic matter

Autochthonous organic matter is the biomass, alive or dead, that is derived in situ from primary production. Although recent studies have demonstrated that autochthonous production cannot support the carbon demand of colored boreal lakes, it is still an important part of the carbon cycling of boreal lakes. In a 13-C whole lake experiment, autochthonous organic matter represented only 13 % of the dissolved organic carbon, but supported 30–65 % of the bacterial production (Kritzberg et al. 2004). Similarly, *Leptodiaptomus minutus*, an abundant copepod in boreal lakes appears to source 35–75 % of its carbon from autochthonous sources. The variation observed was attributed to seasonal and spatial variability (Grosbois et al. 2020). In lakes, including DOC rich boreal lakes, the proportion of autochthonous organic carbon present in sediment can still comprise around 40 % of the organic matter reaching the sediment (Simola 1981). Autochthonous organic matter is particularly relevant as it is in that carbon pool that the fixed 14-C will be found.

5.2.2 Extracellular release

A significant portion (2–50 %) of the total photosynthesis products can be released as extracellular organic matter (Thomas 1971, Thornton 2014). This pool is also increased by organic matter lost during grazing as zooplankton lose a fair share of the intracellular material of their prey. Higher rate of DOC release have been reported for oligotrophic lakes (Fogg 1983).

This share of the detrital carbon is a direct product of the lake primary production, and is composed of molecules such as carbohydrates, proteins, pigments and fats. These substances, also referred to as nonhumic or labile organic matter, are easily metabolized by microbes. Consequently, these secreted compounds are rapidly consumed by microbes, and therefore their concentration at any time is always expected to be low. This organic matter is nevertheless important as it represents an important flux of C from primary producers to heterotrophic bacteria and potentially higher levels of the food web. The range of reassimilated C (that is, C produced by phototrophs and locally transferred to heterotrophic bacterial biomass) varies from 28 to 80 %, of which an average of 50 % (33–78 %) is respired. That is, transformed back to CO_2.

Chemolithoautotrophs are also known to release significant amounts of the carbon they fix in the environment. This can be done actively by exudation or during the lysis of dead cells. It is estimated that in pure culture *Acidithiobacillus ferrooxidans* leaked about 10 % of the carbon it fixed (Schnaitman and Lundgren 1965, Borichewski 1967, Emerson et al. 2013). The importance of these leaks seems to be environment dependent and might be more important in extreme conditions (Ñancucheo and Johnson 2010).

For methanotrophs the importance of extracellular releases is less clear. There are reports of exopolysaccharide production by some methanotrophs, but they are based on selection for industrial purposes or in compost research (Malashenko et al. 2001, Wilshusen et al. 2004, Wei et al. 2015, Tays et al. 2018). Similarly, methanol and formaldehyde can be released or accumulated in the cell when the CH_4/O_2 ratio is low (Harwood and Pirt 1972, Costa et al. 2001).

5.2.3 The allochthonous detrital organic matter

Allochthonous detrital organic matter is terrestrial organic matter imported from the watershed to the lake. It includes aerial deposition, but most carbon is imported by stream and surface runoff. Early spring inflow can lead to a momentary increase in labile organic matter concentration, which, however, is rapidly consumed. So overall the allochthonous fraction of the organic carbon pool is generally considered to be composed of recalcitrant organic matter, often referred to as humic matter (Toming et al. 2013).

This allochthonous organic matter is relevant for understanding the 14-C flux and uptake in lakes. First, it is important to acknowledge that a major part of the CO_2 emitted by lakes is of allochthonous origin. This could be a major factor of $^{14}CO_2$ dilution. Indeed, bacteria appear to mostly respire allochthonous OM, whereas bacterial production and zooplankton growth rely mainly on autochthonous carbon sources (Kritzberg et al. 2004, Cole et al. 2010). The importance of the autochthonous production in the microbial biomass also appears to depend more on total phosphorus, described as proxy for pelagic primary production, than on dissolved organic matter (Steger et al. 2011). However, the respective allocation of allochthonous and autochthonous OM between respiration and biomass is not systematic and could vary seasonally (Steger et al. 2011, Guillemette et al. 2017). When higher levels in the food web are considered, the importance of allochthonous carbon in the biomass could also depend on the environmental and the dietary preference of the fauna. Bilby and Bisson (1992) compared lake systems and noticed that despite higher organic C inputs, lakes with higher allochthonous/autochthonous organic C had lower fish production. The authors concluded that fish populations appeared to depend upon food derived from autotrophic production.

Even though most of the humic acids are of allochthonous origin, autochthonous microbes can modify them, potentially attaching locally assimilated carbon (Tranvik et al. 2000). Humic compounds also play an important role in sedimentation and allochthonous organic matter can represent an important share of the organic matter found in the sediment, with measurements ranging from 55 to almost 90 % (Simola 1981, von Wachenfeldt and Tranvik 2008, Guillemette et al. 2017). The flocculation and sedimentation of allochthonous DOC correlates with several factors, like pH and light (von Wachenfeldt et al. 2009). Von Wachenfeldt et al. (2009) also suggests that while representing only a small portion of the sediment and sediment mass, bacteria might enhance allochthonous DOC sedimentation.

It is also important to consider that the line between recalcitrant allochthonous and labile autochthonous DOM can be crossed. Indeed, solar radiation can blur the border between those two groups. Light can break complex carbon compounds and provide bacteria with labile carbohydrates and nutrients like P and N. But it can also increase binding of labile carbon to humic acids, hence, decrease their availability to bacteria (Tranvik et al. 2000). Both processes are happening simultaneously, but the net direction in which the system goes seems to depend on the lake water chemistry. Based on empirical observations in acidic lakes with low ionic strength, light seems to increase the availability of DOM, whereas in alkaline lakes sun radiation seems to have a negative effect on heterotrophic microbial growth. Tranvik et al. (2000) also showed that in lakes with high concentration of chlorophyll (and supposedly high proportion of autochthonous labile DOM) transformation of labile DOM to humic DOM by solar radiation seemed more important whereas in lakes with dark color bacterial growth was enhanced by radiation.

Finally, the fate of 14-C organic matter with terrestrial origin could be of importance if 14-C is leaking in the whole watershed. While out of the scope of this work, it should be considered when making estimation of the 14-C input in a lake.

5.3 Food web

Freshly produced organic matter can be stored as an energy reserve, or used for maintenance and growth. The produced biomass can then be consumed by grazers to support their biomass and growth. Biomass and energy are, thus, transferred from the microbial biomass and detrital organic carbon toward the micro-, meso- and macrofauna. The importance of the different carbon sources in the different organisms depends on the food preferences of the species, and food availability (Berggren et al. 2018). As both, the diversity of the zooplankton and the available carbon sources, change over time, there is a seasonal variation in the importance of autochthonous and terrestrial carbon sources (Keaveney et al. 2015). For instance, cladoceran (e.g., Daphnia) growth is mostly supported by algae (up to 80 %) and a small proportion of bacteria (cyanobacteria and heterotrophs). But in absence of algae, Daphnia are able to incorporate allochthonous carbon (Galloway et al. 2014, Mcmeans et al. 2015). Furthermore, the source of autochthonous carbon is also important and for instance Daphnia growth is limited when the natural phytoplankton communities are dominated by cyanobacteria. Fish species are also significant in determining zooplankton community (Williams and Moss 2003), but while the composition of both the phyto- and zooplankton is influenced by the fish species present, their total biomass is less impacted (Findlay et al. 2005). When the overall zooplankton biomass was considered in the experimental manipulation of a temperate lake, 22–55 % of its carbon was estimated to be of terrestrial origin (i.e., allochthonous), but when only the particulate organic matter was considered, 40–45 % seemed to be of terrestrial origin (Pace et al. 2004). Based on this information it is tempting to assume that such ratio should also be found in fish. Whereas there is no doubt that terrestrial carbon is found in the upper levels of the food web (Keaveney et al. 2015), it can be argued that the 50 % ratio of allochthonous C might be overestimated. This hypothesis is supported by the work of Weidel at al. (2008) who estimated that autochthonous C in fishes ranges from 47 to 57 %. This might seem to be in line with the values found in Pace et al. (2004), but Weidel et al. (2008) acknowledge that a further 45 % of the carbon is of unknown origin, including both autochthonous and allochthonous carbon.

There is some potential that the importance of terrestrial C is overestimated. First, all the works cited above only consider the mixed epilimnion, hence, not considering the potential autochthonous carbon sources from the metalimnion, which can be significant (see Sections 2.3 and 2.4). Methanotrophs, which are known food, and, thus, carbon, sources to fishes (see below) are neither considered in those studies. Furthermore, as different species have different feeding preferences, the ratio of autochthonous C might vary significantly from one species to another. As this variation is found at all trophic levels, this could potentially lead to some “over accumulators” when 14-C is considered. It is also worth noting that no studies on the carbon origin for other animals that are potential food source for humans like bivalves, amphibians or Crustaceans, was available.

5.3.1 CH_4 derived C

It is now recognized that CH_4 derived carbon represents a significant part of the carbon flux in lakes (Jones and Grey 2011). The methanotrophic biomass, that is, the biomass built by methanotrophs, can represent a least 3 to 11 % of the total bacterial biomass in summer, and up to 41 % in the lower parts of lakes (Bastviken et al. 2003). Up the trophic chain a study focusing on macroinvertebrates in lakes showed that contribution of methane derived carbon was ranging from 0 to 20 % of their biomass (Schilder et al. 2017, Fiskal et al. 2021), but other studies suggest that the contribution of methane carbon could reach 60 % for chironomids and 50 % for daphnia (Jones and Grey 2011). Finally, in a more C deprived environment up to 67 % of stonefly biomass carbon was methane derived (DelVecchia et al. 2016). When higher trophic levels are considered, less data are available. But several studies suggest that some methane derived carbon is transferred up the food web, including up to fish, such as roach (*Rutilus rutilus)*, perch (*Perca fluviatilis*) and pike *(Esox lucius*), that are consumed by humans (Agasild et al. 2014). In the case of the ruffe (*Gymnocephalus cernuus*), which feeds predominantly on chironomids, the proportion of the carbon originating from methane could reach 11.7 % in a situation where profundal chironomids contain 28 % of methane derived carbon, with larger individuals more likely to have a high content of methane derived carbon. In total up to 17 % of the ruffe biomass was estimated to be of chemoautotrophic origin (Ravinet et al. 2010). Finally, it has been demonstrated that fish, such as the European perch (*Perca fluviatilis* L.), have a strong potential to limit CH_4 emissions by consuming grazers that feed on methane oxidizers, indicating that carbon from CH_4 enters the higher levels of the food web (Devlin et al. 2015).

5.4 Sedimentation

Sedimentation is the process whereby particles in suspension settle at the bottom of a water body and, thus, become sediment. In natural water bodies the main force driving sedimentation is gravity. Sedimenting particles can be of mineral or organic nature. Mineral particles include clay, silt, and sand imported from the watershed via the inflow of the lakes. It can also include minerals precipitating *in situ*, such as carbonates of iron oxides. Organic particles include dead microbial cells, dead phyto- and zooplankton as well as dead meso- and macrofauna. It also includes high molar mass organic molecules that have a potential to flocculate. Flocculation was measured to represent 8–22 % of DOC loss in a boreal lake and to be strongly influenced by allochthonous DOC input (von Wachenfeldt et al. 2008, von Wachenfeldt and Tranvik 2008).

Generally, one sinking particle will be a mix of all of the above. A study on a deep humic rich lake in Finland suggested that 40 % of the sedimenting material was of organic matter, with about 40 % of this from planktonic production (Simola 1981). Allochthonous organic carbon represents both an important source of carbon for the sediment but also an important sink of carbon as about 40 % of it might reach the sediment (Hall et al. 2019). When dissolved mineral carbon is included, the burial ratio of the total carbon input is ranging from 2–47 % (Anas et al. 2015). While this indicates that sedimentation is an important factor in carbon storage in lakes, it is important to remember that those values only are relevant for estimating the fate of carbon originating from the watershed. Inflow of dissolved mineral carbon and mineralization of allochthonous organic carbon are likely to have a diluting effect on the 14-C concentration and, thus, lower the uptake of 14-C in primary producers, but could be partly offset by the sedimentation of dissolved mineral carbon and autochthonous organic matter. The latter includes byproducts of chemolithoautotrophy, methanogenesis, methanotrophy and C fixation via photosynthesis. Based on a 14-C incorporation test (added as $NaHCO_3$), 7 to 18 % of the added 14-C remained in the sediment after 11 years, with the highest values measured in eutrophic conditions and the lowest in oligotrophic conditions (Stephenson et al. 1995). The variation observed between oligotrophic and eutrophic lakes was most probably due to C incorporation rates at the time of the 14-C addition (Stephenson et al. 1995). Indeed, in the absence of high photosynthetic activity, most of the added 14-C was lost to the atmosphere. However, this loss to the atmosphere may be less important for 14-C originating from the benthic zone of a lake, as 14-C would have to pass through a full water column with several potential C fixing organism before reaching the surface.

The 14-C amendment experiment by Stephenson et al. (1995), where they inoculated the epilimnion with a $NaH^{14}CO_3$ solution, showed a rapid decrease of 14-C in the sediment with 35 % of 14-C lost after two years. However, the amount of 14-C organic matter was stable after that. This suggests that most of the 14-C OM remaining in the sediment after 11 years is recalcitrant. Another study of a eutrophic brown lake in Finland estimated that 12 % of phytoplankton production was lost to the sediment during the summer stagnation (Simola 1981), but no conclusions were made regarding mineralization of this OM in the sediment. It is also worth noting that organic matter burial is increasing with darker water. Prolonged periods with anoxic bottoms, where mineralization rates are only half of those measured during oxic incubation of sediments, might be responsible for this (Isidorova et al. 2016). This highlight the importance of the hypolimnion in the fate of the organic carbon. This appears particularly relevant as most of the estimations of burial rates of autochthonous carbon only focus on the production in the epilimnion, neglecting both the metalimnion and hypolimnion as potential sources of autochthonous carbon. As described in Sections 2.3, 2.4, and Chapter 3, chemolithoautotrophy, anaerobic photosynthesis and methanotrophy (both aerobic and anaerobic) are known to fix significant amounts of carbon. Their proximity to, and presence in the hypolimnion means that their production is likely less prone to oxidation. These processes could therefore be both, an important filter that removes 14-C from the water column and a source of 14-C to the sediment. In the absence of studies on this topic this is of course only speculation. But as stratification is an important trait of boreal lakes, the differential functions of the epilimnion and hypolimnion on C cycling should not be dismissed.

6 Fate of released carbon

Mineral carbon, i.e., CO_2 and CH_4 are dissolved gases and can potentially leave aquatic ecosystem and be emitted to the atmosphere. The process leading to atmospheric emissions of these gases is the center of a lot of research as both CO_2 and CH_4 are important greenhouse gases that contribute to the climate change. In this report we only consider release to the atmosphere as a potential escape route for 14-C. A previous report analyzing potential flux of 14-C in lakes close to the planned location for radioactive waste repository also considered advection as an escape route (Sobek et al. 2006). However, this export is only a function of the water concentration of C-14 and the runoff from the lake. Thus, the process is considered to be trivial and will not be further discussed in this report. Instead this chapter focus on gas emissions to the atmosphere. There are three main emission pathways: diffusion, ebullition, and storage flux. This section will explore the importance of each pathway for both CO_2 and CH_4. It will also consider the chemistry of dissolved CO_2 and its potential to accumulate in the sediment as carbonate minerals.

6.1 Diffusion

Diffusion is generally defined as the movement of anything from a region of high concentration to a region of lower concentration. In the context of gas in lakes it is twofold. First, it will drive the movement of CH_4 and CO_2 from the sediments and anoxic hypolimnion, where the main CH_4 production happens, toward the metalimnion and epilimnion where concentrations are lower. Secondly, it will also drive CH_4 and CO_2 from the oversaturated water towards the atmosphere. While diffusion is considered the main route for CO_2 emission, its importance for CH_4 is still debated. The relative importance of ebullition for CH_4 escape will be discussed in Section 6.2.

6.1.1 CO_2

CO_2 emissions to the atmosphere are almost exclusively through diffusion. Due to its relatively high solubility in freshwater, 39 mol m^{-3} at 20 °C, CO_2 ebullition is almost nonexistent (Casper et al. 2000). The net air-water exchange of CO_2 depends on the difference in pCO_2 between the water and the atmosphere (Golub et al. 2017) and on the piston velocity (also referred as gas exchange coefficient or gas transfer velocity). The piston velocity (k) can be affected by several variables including wind, currents, wind fetch (length of water surface in the wind direction), surfactants, and rainfall. K is generally based on empirical values, and several models are used to determine it. What model is the most relevant depends on the studied system (Gålfalk et al. 2013, Klaus and Vachon 2020). While figuring out what model would be the most relevant is out of the scope of the report, it is important to notice that all of the variables influencing k are potentially influenced by both climate change and/or vegetation change around the lake.

Putting aside the human made increases in atmospheric CO_2, the key variable to determine difference in pCO_2 between the water and the atmosphere is the pCO_2 in the epilimnion. The concentration of dissolved CO_2 is regulated by four key processes balance between respiration and carbon fixation, that is, in the epilimnion, photosynthesis (Engel et al. 2020). Respiration and carbon fixation in deeper water (i.e., meta- and hypolimnion) will influence the surface pCO_2 via the diffusion of CO_2 from the layer with the highest pCO_2 to the layer with the lowest pCO_2. Therefor chemolithoautotrophy, methanotrophy and anoxic oxidation of organic matter also have a potential impact on surface pCO_2. Previously mentioned increases in DOC as well as increases in temperature are also expected to increase CO_2 emissions to the atmosphere (Nydahl et al. 2020).

Lakes, and particularly humic ones, are generally oversaturated in CO_2, but during blooming events high CO_2 fixation rates can lead the CO_2 partial pressure in the lake water to drop well below atmospheric level. In such situation the net CO_2 flux is inverted (Emerson et al. 2011). Net flow of CO_2 from the atmosphere to the water can also happen in lakes with very low allochthonous (mineral and/or organic) carbon sources, similarly to what happens in the oceans.

If pCO2 is a key parameter to estimate global emissions from lakes, the exact mechanisms allowing CO_2 to escape water are still under investigation. Wind, water movement, pH and DOC are all parameters with a potential to influence the transfer of CO_2 to the atmosphere. Consequently, diffusive flux varies highly through time.

6.1.2 CH_4

The importance of CH_4 diffusion varies from lake to lake and can represent as little as 4 % of methane emission (Casper et al. 2000, Walter Anthony et al. 2010). However a study over 13 lakes in Quebec suggests that on average diffusion is responsible for 44 % of emission and that in lakes deeper that 3 m ebullition is negligible (DelSontro et al. 2016) . Furthermore, the origin of the CH_4 diffusing to the atmosphere is unclear, but the methane paradox (see Section 3.1) and the work of Bižić et al. (2020) suggest that it might be a product of oxic methanogenesis in the epilimnion. It is therefore possible that diffusion from the hypolimnion to the atmosphere is limited, which would be in line with the low diffusion rate of methane in water as well as the efficacity of aerobic methanotrophs (Bastviken et al. 2004a, Moradi et al. 2020).

6.2 CH_4 ebullition

As CH_4 has a relatively low water solubility, 1.237 mM at standard conditions, (Wiesenburg and Guinasso 1979), ebullition is potentially an important route of escape for CH_4 produced in the sediment. As it is a more direct and rapid route to the atmosphere, it has a potential to bypass the metalimnion biofilter (see Section 3.2). But while recent works suggest that focusing on diffusive emissions might have caused a ~300 % or more underestimation of CH_4 emissions (Walter Anthony et al. 2010, Sanches et al. 2019), the importance of ebullition in lakes is still unclear as ebullition rates appear to vary strongly on seasonal and daily basis (Fechner-Levy and Hemond 1996, Goodrich et al. 2011). Different studies suggest that contribution of ebullition to the total CH_4 emissions from boreal lakes is small (in the range of 2–5 %) (Männistö et al. 2019) or in between those extreme values (18–22 % of total emissions) (DelSontro et al. 2016). The controversy might come from the temporal and spatial variation in ebullition.

Even though most gas escaping ocean sediment as bubbles can potentially be dissolved and consumed by methanotrophs, this is more likely to happen in deep water areas (> 100 m) (McGinnis et al. 2006). This is notable as ocean global flux is dominated by emission from shallow environments (Weber et al. 2019). However, the 100 m limit observed in the ocean might not be relevant for northern lakes as several studies measured little if no contribution of ebullition to emission in lake areas deeper than 3–6 m (DelSontro et al. 2016, West et al. 2016). Another critical aspect in determining the importance of ebullition is the trophic state of the lake. Phosphorus rich productive lakes are expected to emit more CH_4 via ebullition (DelSontro et al. 2016), but phosphorus might allow higher CH_4 oxidation rates especially under the ice water during winter, hence, limiting the escape of CH_4 bubbles to the atmosphere (Sawakuchi et al. 2021). Besides the trophic status, rapid changes in temperature and pressure as well as precipitation (i.e. rain) are considered as factors responsible for ebullition events potentially leading to important CH_4 releases to the atmosphere (Tokida et al. 2007, Männistö et al. 2019).

More critically, the type of ebullition is important too. Indeed the spatial variations described by Walter Anthony et al. (2010) depend on the type of ebullition. In fact, 87 % of the CH_4 emissions they detected was from a discrete seep, while background ebullition represented only a small portion of CH_4 flux. This suggests that even though ebullition is an important process to understand CH_4 emissions of lakes in a climate change perspective, it might be less relevant for $^{14}CH_4$ flux. Indeed, ebullition has a strong potential for allowing important volume of CH_4 to bypass the biological filter described in Section 3.2, which can represent an important source for atmospheric CH_4. However, even though its relevance is limited in space and time, it might have little impact on the $^{14}CH_4$ flux that is more likely to be "slow and steady" and spread throughout the whole surface of the lake. If the emission for $^{14}CH_4$ were concentrated in time and or space, the probability that a 14-C seeping site coincide with an ebullition site is, at best, very low (Walter Anthony et al. 2010). It seems therefore likely that only a limited amount of $^{14}CH_4$ could escape the lake via ebullition.

6.3 Storage flux

Storage fluxes refer to sudden releases of dissolved gas, typically when water is mixed. Causes of storage flux are diverse. However, the most common and regular event leading to storage flux is the seasonal mixing, or overturn, of lakes. In the spring and autumn, a rapid change in temperature impacts surface water temperature and, hence, water density. These changes, often in combination with increases in wind and precipitation, drive the mixing of the different layers of a lake. The frequency of these events varies from lake to lake, but when it happens, it generally leads to a major gas release. This can be particularly significant as both CH_4 and CO_2 are known to accumulate in the hypolimnion, thanks to the low permeability of the metalimnion as well as to the higher pressure. Similarly, both CH_4 and CO_2 can accumulate under the ice in the winter and are released during the ice off (Jonsson et al. 2001, Denfeld et al. 2015, Ducharme-Riel et al. 2015).

Overturn is often considered to be a major source of atmospheric release of methane. Almost all (over 95 %) of dissolved methane can be lost during the autumn overturn (Encinas Fernández et al. 2014), but the fate of that lost methane is less clear. Encinas Fernandez et al. (2014) estimated that only 40 % of the methane was lost to the atmosphere, and some other groups have estimated that the methanotrophs have the potential to oxidize most of the methane even during the overturn (Graf et al. 2018, Mayr et al. 2020c). It is therefore very likely that the efficiency of the methane filter is maintained, at least partially, during overturn.

Net CO_2 release during autumn mixing and during spring ice off are considered major sources of atmospheric CO_2. In a study based on 15 temperate and boreal lakes CO_2 emissions during spring ice off accounted for 3 to 80 % (average 17 %) of the annual net CO_2 flux (Ducharme-Riel et al. 2015). In the same study, end of summer hypolimnetic release accounted for 1.4 to 46 % (average 10 %) of the yearly emissions (Ducharme-Riel et al. 2015). This translates to an average 404 mg C m^{-2} d^{-1} emitted during ice off and 228 mg C m^{-2} d^{-1} during autumnal mixing. However, in the context of boreal lakes, it is not clear if the extra CO_2 emissions measured in the autumn and spring are due to storage flux or increased mineralization due to the oxygenation of anoxic water (Bellido et al. 2009). In any case, a change in the seasonal pattern could lead to a change in the CO_2 and CH_4 storage flux.

6.4 Carbonate precipitation

Dissolved inorganic carbon is a mix of free CO_2 (a gas), the bicarbonate ion (HCO_3^-), and the carbonate ion (CO_3^{2-}). The proportion of each component depends mostly on pH (Figure 6-1), but the carbonate system can also act as an important buffer with strong impact on pH. Overall low pH means that CO_2 dominates whereas at high pH the balance goes toward carbonate ions. For instance, at pH 5.3, only CO_2 is present in significant quantities; at pH 6.3, CO_2 and HCO_3^- are in equal quantities and CO_3^{2-} is effectively absent; at pH 7.3 there is ten times as much HCO_3^- as CO_2 and at pH 8.3 there is one hundred times as much HCO_3^- as CO_2. At all these pHs, CO_3^{2-} is in very low proportion and it will reach a concentration equal to HCO_3^- only at pH above 10. In the absence of other acids or bases a change in the concentration of these ions is the main driver of pH. For instance, CO_2 fixation by phytoplankton would lead to a pH increase, whereas atmospheric CO_2 invasion or respiration would lead to a pH decrease. Similarly, addition of solid carbonate rock (e.g., limestone) would consume CO_2, as it dissolves, and release more HCO_3^- ions and increase the pH ($CaCO_3 + CO_2 + H_2O \rightleftharpoons Ca^{2+} + 2\ HCO^-_3$). This also means that the precipitation of dissolved carbonate ion into solid phase carbonate will release CO_2. The main sources of DIC in lakes are mineralization of organic matter and lateral flow.

In karstic watersheds the main source of carbonates in the sediment is undissolved particles of minerals brought into the lake laterally. However, dissolution of carbonate releases Ca^{+2} or other ions, which can (re)precipitate dissolved carbon depending on the conditions. This dissolution reprecipitation process has a potential to trap 14-C in the sediment.

Biomineralization is the production of minerals occurring as a result of biological activity. The formed minerals are diverse, including phosphate, silicate, sulfate, carbonates and more (Weiner and Dove 2003, Ehrlich et al. 2021). Even though processes leading to several of these minerals could indirectly influence the carbon cycle by depleting nutrients (e.g., precipitation of phosphate or iron), the most relevant aspect of biomineralization in the context of 14-C leak into boreal lakes is the formation and subsequent sedimentation of carbonates in tissues. Other biominerals containing carbon, like carbonated hydroxyapatite (present in bones and teeth of vertebrates) or organic crystal, can also have an important environmental impact (Martin et al. 2012) but do not seem to be relevant in this context. Furthermore, even though biomineralization plays a major role in ocean carbon chemistry (Eichenseer et al. 2019) it is not as important in freshwaters. While the origin of carbonates in the sediment in freshwaters is still discussed (Rodina et al. 2021), it is generally accepted that biogenic carbonates only represent a major source of carbonates in soft water lakes whereas inorganic precipitation dominates in hardwater lakes. However blooming events can lead to "whiting event" where cyanobacteria locally increase the pH leading to calcification around their cells. This process can be an important source for carbonates in lake sediment, but is probably only relevant when the watershed bedrock is karstic (Thompson et al. 1990). It could also be a source of 14-C concentration as phytoplankton preferentially take up 12-C, hence, leading to higher concentration of heavier C isotopes in the precipitating calcite (Thompson et al. 1997).

As the stability of carbonates depends on water chemistry, particularly on pH and carbonate saturation, the importance of $CaCO_3$ precipitation in acidic boreal lakes is in general minimal. Photosynthesis can increase the pH and favorize carbonate precipitation but crystals produced in acid boreal lake conditions are likely to dissolve as they sink in water with low carbonate saturation (Kelts and Hsü 1978). Furthermore, the current trend of brownification observed in boreal lakes might decrease the importance of $CaCO_3$ in boreal lakes as it decreases the pH and photosynthesis (Nydahl et al. 2019). In the case of hardwater lakes, such as those in Forsmark, the presence of Ca^{+2} ions can lead to formation and precipitation $CaCO_3$. It is therefore not surprising that carbonates are present in the sediment of that lake (Andersson 2010). In such conditions, the photosynthesis induced precipitation of $CaCO_3$ could also lead to accumulation of $CaCO_3$ in the sediment. This process could become more important in the future as the frequency, magnitude and duration of cyanobacterial blooms is increasing (Huisman et al. 2018).

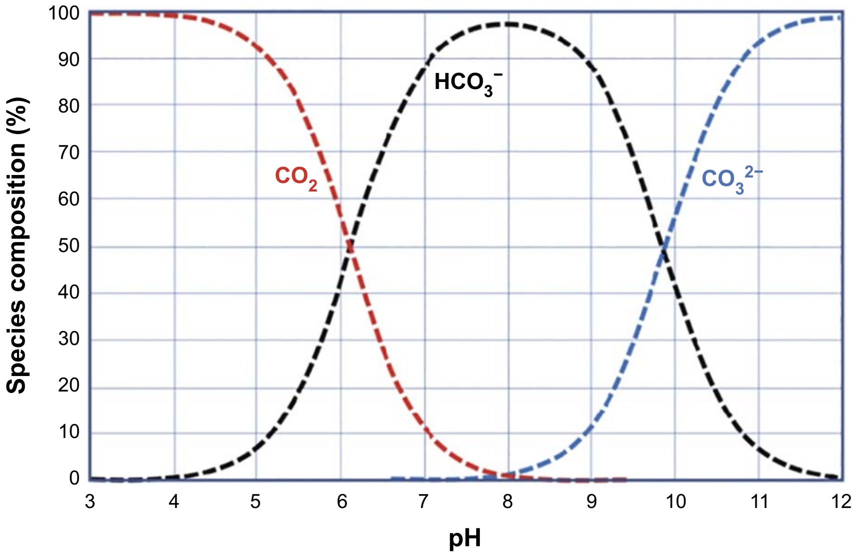

Figure 6-1. *Bjerrum plot for dissoved CO_2 showing the relative proportions of [HCO_3^-], [CO_3^{2-}] and [CO_2] to DIC in seawater relative to pH at 25 °C. Here, CO_2 includes dissolved molecular CO_2 and H_2CO_3. The graph clearly shows that when CO_2 is depleted, pH rises (Rohling 2023). Figure available via license: Creative Commons Attribution 4.0 International.*

7 Specificity of shallow lakes

Whereas all the processes described so far could be present in any kind of lake, their potential importance varies depending on the lake type. Chemical parameters like pH, salinity, nutrient concentrations (e.g. phosphorus or nitrogen) or organic carbon concentration, for instance, have a strong impact on primary production, respiration and carbonate precipitation. Physical variables like temperature, wind and sun exposure can also have an impact on stratification and oxygen levels. Similarly, lake morphology is an important parameter for understanding how elements are cycled in a lake. This is particularly relevant for carbon cycling as both, the area and depth of a lake, can have a significant influence on the organisms mainly responsible for primary production. This section will explore how the specific properties of shallow alkaline lakes can influence the carbon cycle.

7.1 Importance of the benthic and littoral zone

Contrarily to bigger and/or deeper lakes, where benthic primary production can be considered as marginal, in shallow lakes benthic zone can contribute most of the primary production. This is possible as most, if not all, of the benthic habitats are in the euphotic zone, allowing the development of vegetation and other photosynthetic organisms. In some lakes the sediment can be covered by a microbial mat composed of cyanobacteria, or by submerged macroalgae like *Chara sp*, which may extend up to 20 cm above the bottom of the lake (Andersson and Kumblad 2006, Genkai-Kato et al. 2012). However, shallow lakes can go through shifts between alternative states. One state is a clear water state dominated by benthic primary production; the other is a turbid state where the production is dominated by phytoplankton. It is generally accepted that the main cause of the shift is nutrient concentration, where higher concentration triggers a shift toward a turbid (i.e. phytoplankton dominated) system. However, other variables like climate and lake morphology also play a role (Scheffer and van Nes 2007). That same review interestingly points to an alternative state, where the primary production is dominated by charophytes (i.e. *Chara* species). While it is not clear what triggers the shift toward a charophyte dominance, it seems that the efficiency of charophytes in consuming DIC allows it to outcompete other primary producers (van Nes et al. 2003). Charophytes are so efficient in capturing DIC that they are associated with high pH increase (> 10) and carbonate precipitation (Pentecost et al. 2006). Overall, submerged macrophytes in clearwater lakes seem to be particularly efficient in burying carbon in sediments (Kufel et al. 2020). Not only do they have high primary production yield, but they also have higher carbon retention yield in anoxic conditions compared to phytoplankton (26 % vs 1 % in experimental conditions) (Domine 2011). This specificity of submerged macrophytes is even more important in clear hard water lakes dominated by charophytes as they also have a strong potential to increase carbonate precipitation (Pukacz et al. 2014). This may explain why lake Eckarfjärden is under-saturated in CO_2 during parts of the year and overall a net autotrophic ecosystem (Andersson and Kumblad 2006). More detailed information on sedimentation rates for lake Eckarfjärden can be found in a previous report written by Eva Andersson (Andersson and Kumblad 2006; Andersson 2010).

While the role of charophytes, or other submerged macroalgae, in incorporating CO_2 into aquatic biomass is well documented, it is not the case for their importance in the methane cycle. Submerged macroalgae could impact CH_4 production and consumption in several ways. By producing large quantity of biomass, they could support CH_4 production by providing substrate to the methanogens; and by increasing heterotrophic respiration and, hence, helping to create anoxic conditions. They could also limit dredging, which is a known factor impacting methane emissions in shallow lakes (Nijman et al. 2022). Submerged macroalgae could also mitigate CH_4 emissions by providing the O_2 necessary for methane oxidation, by limiting P availability and by shading (hence cooling) the sediments (Schmiedeskamp et al. 2021, Nijman et al. 2022). Overall, it seems that in shallow lakes vegetated areas can act as net sink for both CO_2 and methane, whereas bare areas tend to be net sources (Ribaudo et al. 2017, Schmiedeskamp et al. 2021). Furthermore, shallow lakes in the clear phase, that is when primary production is dominated by macrophytes, are associated with lower CH_4 emissions (Zhou et al. 2020).

Charophytes are also important for the fauna as they provide protection of fish fry, and a source of food, both for aquatic animals and birds (Bicudo et al. 2013). For instance, in Spain the exotic crayfish *Procambarus clarkii* Girard feed preferentially on charophytes, and herbivorous waterfowl have been seen feeding on charophytes stands (Rodrigo et al. 2015). While it is very likely that fish and benthic invertebrates also feed on charophytes, there is no clear evidence and no data regarding the proportion of fish biomass originating from these macrophytes (Rodrigo et al. 2016). Interestingly, a study based on 11 temperate oligo-mesotrophic hardwater lakes in northern Germany showed that charophyte biomass was better correlated with *Abramis brama* than with herbivorous rudd (*Scardinius erythrophthalmus* L.). *Abramis brama* are fishes, which are omnivours, feeding on larvae, bivalves and other benthic animals, as well as plants and phytoplankton (Alirangues Nuñez et al. 2023). Even though the causal link between the *Abramis* and *Chara* biomass is not clear, there would be a potential for accumulation of carbon assimilated by charophytes in *Abramis* biomass. This seems even more likely as *Abramis brama* are known to bioaccumulate heavy metals, even in low contaminated sites (Farkas et al. 2003). *Abramis*, also known as common bream, are not considered particularly palatable, but being of relative big size and easy to catch, it used to be a staple during the middle ages (Rambourg 2006). They are now used for biogas production, as feed for other fish and considered as a sustainable alternative for imported fish (Svensson 2019, Ringborg 2022). It is worth noting that there is currently a drive to remove bream from Swedish lakes in order to limit P levels in lakes in Östergötland and a will to promote their consumption by human (Svensson 2019). This means that the potential risk of 14-C contaminated fish being consumed by humans could increase if similar projects were implemented in Forsmark area. *Abramis brama* might not be present in Forsmark area, but similar issues could arise for any fish species with similar ecology and feeding habits.

The littoral part of the lake, that is, the zone with emergent macrophytes, can also represent an important part in shallow lakes as this kind of vegetation can grow in water depths up to 0.7 m. In the case of lake Eckarfjärden 30 % of the lake area is dominated by emergent macrophytes. As most of the production of emergent macrophytes happens above the surface and the water is likely DIC depleted during the productive season, it seems unlikely that they consume much of $^{14}CO_2$. However, macrophytes play an important role in the methane cycle of lakes. They provide an important source of organic matter via their litter and underground biomass which favorize CH_4 but also provide an escape route for methane (Chanton et al. 1993, Whiting and Chanton 1996). This could potentially have a diluting effect on $^{14}CH_4$ leaking through the littoral part of the lake and increase its escape to the atmosphere. However, this seems to be more important where CH_4 emissions are limited. When vegetation is abundant and substrate not a limiting factor for methanogens, temperature appears to be a more important factor to predict CH_4 flow from littoral part of boreal lakes (Kankaala et al. 2005). While these factors might decrease the risk of 14-C accumulation in the food web, this could be limited by the fact that fish from macrophyte dominated areas of lakes might depend more on CH_4 derived carbon in such systems (Agasild et al. 2014).

7.2 Stratification in shallow lakes

It has long been recognized that shallow lakes are constantly mixed and show little to no stratification. Recent works, however, show that shallow lakes can have a daily cycle of stratification during the day and mixing during the night. This stratification is not only thermal, but also chemical with the daily development of anoxic water layer at the bottom of shallow lakes (Andersen et al. 2017, Martinsen et al. 2019, Sand-Jensen et al. 2019). This daily cycle of stratification is creating a carbon pump where photosynthesis induced calcite precipitation and freshly produced OM sink in the anoxic bottom. There OM is oxidized and calcite is dissolved. Both process increase CO_2 in the anoxic layer, allowing replenishing the CO_2 depleted upper layer when night mixing occurs (Andersen et al. 2019). This diel cycle is probably also important for phosphorus as it can precipitate with carbonates and is part of the sinking biomass (Sand-Jensen et al. 2019). Furthermore, anoxic conditions are also favorable for a release of metal (Fe, Al) bound phosphorus, but this would only be a source of P if the sediment is rich in P (Søndergaard et al. 2003). All in all, the cycle of daily stratification plays an important role for the primary production of shallow lakes, allowing primary producers to avoid limitation in both P and DIC.

While important, this daily cycle appears to vary with season. In a study of nine small, shallow and slightly alkaline lakes in Denmark stratification was observed on 47 % of the days during the entire year and 64 % of summer days (Martinsen et al. 2019). Both, meteorological variables and lake morphology appeared to be important predictors for the stratification on a given day. Diel stratification was more likely to happen when air temperature, irradiance, and maximum depth were high and if wind speed and lake area were small. Regarding chemical (O_2) stratification, the presence of benthic vegetation seemed to be a critical variable (Vilas et al. 2017). Indeed, dense submerged vegetation both allow for high O_2 in the top layer while limiting turbulence and light penetration in de facto colder bottom water. It also increases respiration by providing organic matter (Andersen et al. 2017).

Daily stratification-mixing cycle also means that a short-lived metalimnion appears and disappears. Unfortunately, there is no literature on the productivity of those short-lived metalimnia. This is not a surprise as the importance of non-oxygenic primary production is often dismissed in lakes (Obrador et al. 2014). While dissolved oxygen yields a good and easy estimate of oxygenic primary production, such estimates are very likely to underestimate the total primary production (Camacho et al. 2001, Casamayor et al. 2012). However, both primary production and respiration at the metalimnion vary greatly in shallow lakes, from 0 % to 87 % and from < 1 % to 92 %, respectively, of the whole lake gross primary production (Giling et al. 2017), and a survey of stratified boreal lakes suggests that at least chemolithoautotrophy needs a stable stratification to thrive (Martin 2021).

Overall, the quick succession of stratification and mixing in shallow lakes means that they have a very specific biogeochemistry. Indeed, clear and shallow lakes go through a succession of rapid depletion of DIC and phosphorus followed by rapid mixing phase allowing a replenishment of elements necessary for photosynthesis. This might further explain why such lakes tend to be net autotrophic (Andersson and Kumblad 2006). It is unclear how this regime of mixing affects methanotrophy, but as described in Section 3.2, methanotrophs have the potential to consume methane during mixing phases (Graf et al. 2018, Mayr et al. 2020b). However, these considerations are generally dismissed when methane emission from shallow lakes are considered. It is generally accepted that ebullition is the main emission source in shallow lakes, where the biofilter is inefficient in limiting ebullition (DelSontro et al. 2016, West et al. 2016). The potential importance of ebullition for 14-C escaping towards the atmosphere is described in Section 6.2.

8 Conclusion

Carbon fluxes (Figure 8-1) from one pool to another (e.g., from organic to inorganic) as well as from one compartment to the next (e.g., from the hypolimnion to the metalimnion, or from epilimnion to the atmosphere) vary significantly in time and space. Processes allowing fast release of dissolved gases, such as mixing, heavy rainfall or fast change in atmospheric pressure will increase the portion of CO_2 and methane that can reach the atmosphere, but this fraction will also be modified by nutrient availability, climate, weather, lake shape and fauna. Even in relatively poor nutrient conditions, microbes have the potential to incorporate a considerable part of the available mineral C (including CH_4). It appears therefor likely that on a short term perspective a substantial part of the released 14-C will be incorporated into the lake biomass (Stephenson et al. 1995, Bastviken et al. 2008). The further fate of this 14-C will, thus, depend on mineralization rates, growth yield, and vertical migration of the 14-C. With that in mind, key factors are the importance of C dilution by allochthonous minerals (i.e atmospheric CO_2 and dissolved carbonates) and organic C sources, and food web C incorporation. In watersheds rich in calcareous rocks precipitation of carbonates could also be a significant process.

In the absence of fast release events, some 14-C will likely accumulate in the sediment. Even if lakes tend to be net CO_2 emitters, a significant part of the dissolved CO_2 is expected to be incorporated in the biomass. Although it is difficult to extrapolate values from one lake to another lake, the best available data suggest that at least 7 % – 18 % of fixed carbon could be in a long-term storage in the sediment (Stephenson et al. 1995). But these values only consider a productive epilimnion and ignore the processes in the hypo- and metalimnion, where 14-C is more likely to be processed. This also does not consider the potential for carbonate precipitation in alkaline lakes. It is important to acknowledge the 14-C storage in the sediment as it is a long term process and storage that can last over several millennia (Chmiel et al. 2015).

There is also no doubt that some 14-C will go through the food chain and end up in potential food sources to humans and other vertebrates. Literature suggests that autochthonous organic matter, where 14-C will be found, is the preferred food source for aquatic fauna. The concentration of 14-C in potentially edible organisms would then depend mostly on the ratio of 14-C/12-C in the water.

The frequency of fast release events (i.e. mixing) to the atmosphere is of particular relevance. Indeed, frequent events would regularly deplete the 14-C stock of a lake and limit the possibility of accumulation in the sediment and along the food web. Frequent fast releases would, hence, work as a pump for moving mineral 14-C from the water to the atmosphere. However, less frequent mixing might increase the importance of local cycling and recycling of carbon in the hypolimnion. In such conditions the 14-C/12-C ratio could increase as the 12-C pool would remain the same while 14-C keeps seeping in the system. This could then favorize accumulation of 14-C in the sediment and the upper levels of the food web. Furthermore, it could lead to an accumulation of 14-C gases in the hypolimnion. Rare mixing events could create gusts of 14-C rich in CO_2 to the atmosphere.

In clearer alkaline lakes phytoplankton blooming events and macrophyte growth could have the opposite effect of release events. Indeed, the associated precipitation of calcium carbonates combined with the reduction of mineral carbon to biomass would also deplete the dissolved mineral 14-C stock. But contrarily to release events, the pump effect would move the radioactive C from the water to the food web and sediments (see Chapter 7). Another important difference is that whereas release events have the potential to release both CO_2 and CH_4 stock to the atmosphere, phytoplankton bloom would only impact CO_2 (and its dissolved forms). Methanotrophs also have a potential to bloom at chemocline (see Section 3.2), but this having no direct impact on CO_2 concentration, it should not lead to carbonate precipitation, and, hence, only has a pumping effect of 14-C incorporated in CH_4.

Carbon cycling and the fluxes in lakes are complex and encompass numerous biological, chemical, and physical processes. Several of these processes are poorly studied (e.g., the importance of primary production in the metalimnion) or particularly difficult to model (e.g., gas ebullition or humic acid chemistry). However, a detailed understanding of all processes is not necessary to model a system, and therefore a “black box” approach could be more relevant, and *in situ* measurements of C flux could give a good picture of the fate of 14-C in a specific lake. Considering the variability between lakes it is also probably the only realistic option to precisely determine the fate of 14-C in a specific lake.

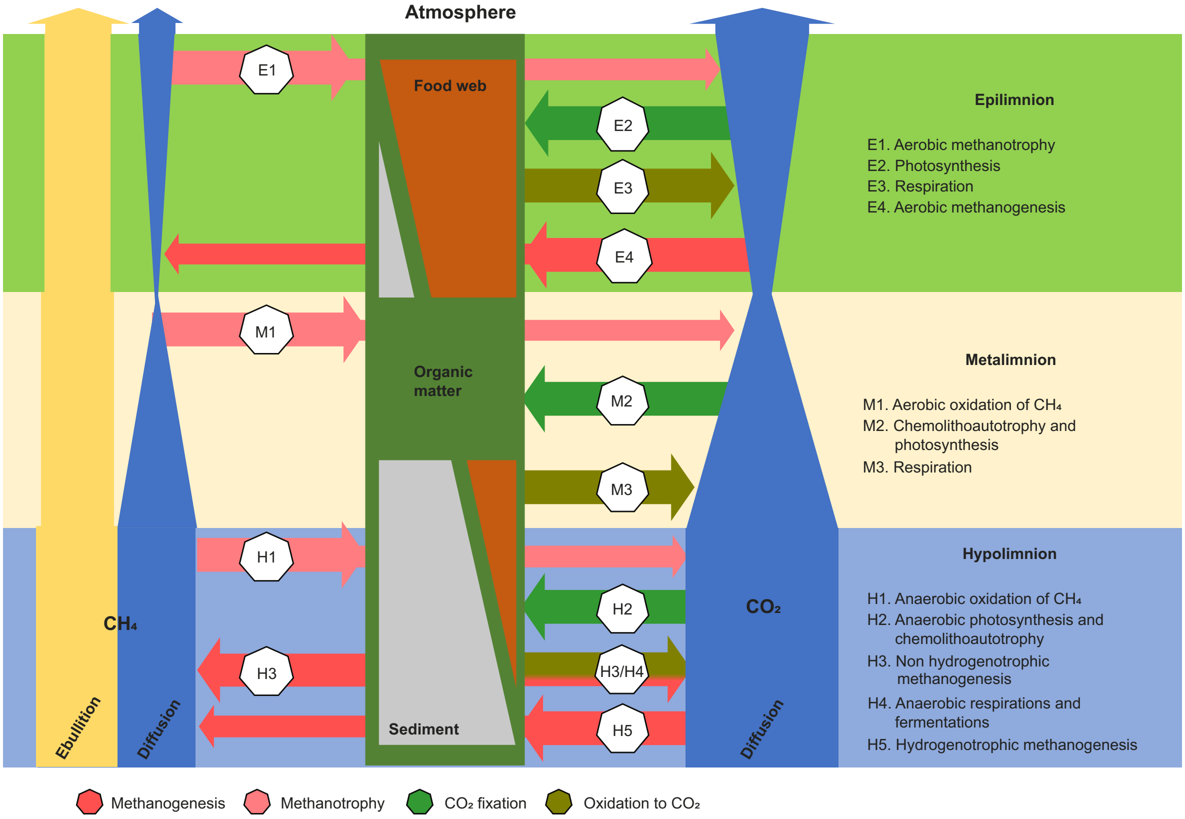

Figure 8-1. *A schematic representation of the main biological processes of carbon cycling in a stratified lake with anoxic hypolimnion. Horizontal blocks represent the layers of a stratified lake (not to scale), vertical blocks the main pools of carbon and horizontal arrows the biological process moving carbon from one pool to another. Relevant biological processes for each layer are described on the right-hand part of each block. Widths of the horizontal arrows do not reflect the relative importance of each process. Arrows continuing under the organic matter block indicate that a process incorporates only a part of the carbon while the rest is oxidized or reduced for energy (note that acetoclastic methanogenesis (H3) splits the substrate to* CO_2 *and* CH_4*). Changes in vertical width of gas pool show the general trend for gas concentration in a specific layer but are not to scale. The central pool (organic matter) includes all forms of organic matter, dissolved and particular; live and dead. The inner triangles indicate possible pools for accumulation of organic carbon and their base is situated in the layer where it is most likely to be of relevance. Food web includes all organisms that are not primary producers.*

If such approach was undertaken, it is however critical to understand what elements of the system are relevant. With that in mind it appears that a major black spot of the existing literature is the fate of the carbon fixed in the metalimnion or in the redox layer of microbial mats. Indeed, C transfer between the different layers is slow and the redox layers of aquatic systems have a potential to trap a significant share of the 14-C leaking from the sediment. Therefore, any further investigation on the fate of 14-C in lakes should consider the impact of stratification on the biological and physical flux of C. It seems also important to consider that insufficient measurement frequency of carbon fluxes can miss important but sudden events leading to significant shifts in the carbon stocks, like major mixing events (e.g. during storm or ice-off) or planktonic blooms. The importance of these sudden events should not be dismissed as the frequencies of both extreme weather events and blooms are increasing (Huisman et al. 2018, Fischer et al. 2021). Efforts to better understand the importance of redox layers and of events would not only be valuable for the improvement of geological repositories safety, but also for the general understanding of carbon cycling in boreal lakes.

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