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Lake eutrophication dynamics and indicators in the boreal zone: case examples from Finland

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This review describes the tracking and assessment of eutrophication in boreal lakes, using Finland as an example. The coverage of key ecosystem components sensitive to eutrophication in the ecological status assessment was evaluated. Key approaches for the assessment of these components are reported and discussed to offer a comprehensive view of eutrophication dynamics in Finland as a good example of cold climate regions sensitive to climate change. Our review revealed that, whereas parameters included in the monitoring schemes of the Water Framework Directive (water quality, phytoplankton, benthic invertebrates, macrophytes, and fish) were frequently addressed by Finnish eutrophication studies, other relevant indicators were also included. Such parameters include zooplankton and the overall quality of the sediment, which offer key insights into internal nutrient loading and help define a lake's reference conditions. The discussion highlights overlooked issues in ecological assessments and offers recommendations for improving eutrophication assessment and guiding future monitoring and research.

Introduction

Eutrophication is one of the main causes of degradation of lake water quality. Eutrophication often leads to increased primary production with increased abundance and biomass of phytoplankton, proliferation of cyanobacterial blooms and excess coverage of macrophytes (Burkholder *et al.* 2007; Vinçon-Leite and Casenave 2019). Increased degradation of autochthonous organic material increases oxygen depletion and enhances the risk of anoxia, consequently threatening the survival of fish and benthic invertebrates and increasing the risk of internal loading. Eutrophication also decreases the value of both the provisional (water abstraction) and cultural (recreation) aquatic ecosystem services (Smith *et al.* 2002; Gordon *et al.* 2010).

Eutrophication on lakes results from excessive inputs of nutrients, mainly phosphorus (P) and nitrogen (N) (Howarth and Paerl 2008; Schindler *et al.* 2016; Dang *et al.* 2023). Excess loading mainly originates from changes in land-use (Mehdi *et al.* 2015; Marzecová *et al.*

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2017; Choi *et al.* 2024), insufficient treatment of wastewaters (Ulén and Weyhenmeyer 2007; Vargas-González *et al.* 2014) and unsustainable use of fertilizers (Withers *et al.* 2014). Concerns about climate change and its impacts on the trophic state of lakes in the Northern Hemisphere have increased in cold climate regions. Increase in average temperatures together with higher precipitation and runoff, lengthening of the growing season, and enhanced thermal stability are highlighted as the climate change driven factors exacerbating the impacts of eutrophication (Gros *et al.* 2023; Botrel and Maranger 2023; Zhao *et al.* 2024a). However, studies which specifically covered eutrophication in less populated countries where anthropogenic pressure is much smaller than in other cold climate regions regions have been understudied relative to the vast number of lakes (Gros *et al.* 2023).

In the European Union (EU) Member States, the Water Framework Directive (WFD) is the major policy instrument driving the protection and restoration of lakes, with a target set to achieve good or high ecological and chemical status of surface waters by 2027. Ecological status is evaluated in comparison with a water body of a similar type in a natural state that displays no or very little human impact and, thus, by definition, represents high status. In connection with the implementation of the WFD, EU Member States perform chemical and biological monitoring and assessment of lakes on a regular basis. The assessment of ecological status largely reflects the state of eutrophication and primarily concerns biological quality based on the five biological quality elements (BQEs): diatoms, phytoplankton, benthic invertebrates, macrophytes and fish (e.g., van Puijenbroek *et al.* 2015). However, some relevant organismal groups, such as zooplankton are not included in systematic WFD monitoring activities (Jeppesen *et al.* 2011) and the impacts of lake deterioration may not be fully discovered with current metrics.

Here, using Finland as an example, we aimed to assess indicators by which eutrophication has been assessed, and evaluate how broadly WFD-related indicators cover the symptoms in related studies. By reviewing the literature, we discuss how eutrophication manifests in Boreal lakes and whether all the symptoms of eutrophication are covered in eutrophication-related monitoring activities under WFD. Finally, we suggest additional parameters that should be considered when assessing eutrophication and setting targets for lake managers.

Methodology

The initial step of the review was to conduct a thorough literature search using academic databases and search engines, including Scopus, Web of Science (WOS), and Google Scholar, to find papers about eutrophication in Finnish lakes. No filter for publication year or citation was considered. The search terms used were "lake", "eutrophication" and "Finland" and the search was limited to topics covering the title, abstract, and keywords of the papers. The last search access date was 22 January 2025 and all published articles before this timeline found by the search have been considered in the review process. Irrelevant papers were thereafter eliminated by screening the titles and abstracts of the articles to determine their scope, i.e. whether they described the impacts of eutrophication in Finnish lakes or not. After the screening process, we imported relevant articles to VOSviewer software, developed by (van Eck and Waltman 2010), to visualize the co-occurrence between terms related to the eutrophication of Finnish lakes and find the most repetitive keywords. Accordingly, we determined three to be the minimum co-accordance of the keywords. The VOSviewer classifies the keywords in different colors. The keywords that are closely related to each other and co-occurred more will have the same color.

In the next step, we comprehensively reviewed the papers to extract key information regarding our research questions. The identified literature underwent a rigorous screening process to select studies that are relevant to the present study in terms of subject and research objectives, resulting in 82 articles with 45 lakes across Finland. These lakes were classified based on their morphometric characteristics and summer mixing regimes. This is because the small and shallow lakes usually have faster thermal responses, more frequent mixing and consequently, stronger sediment-wa-

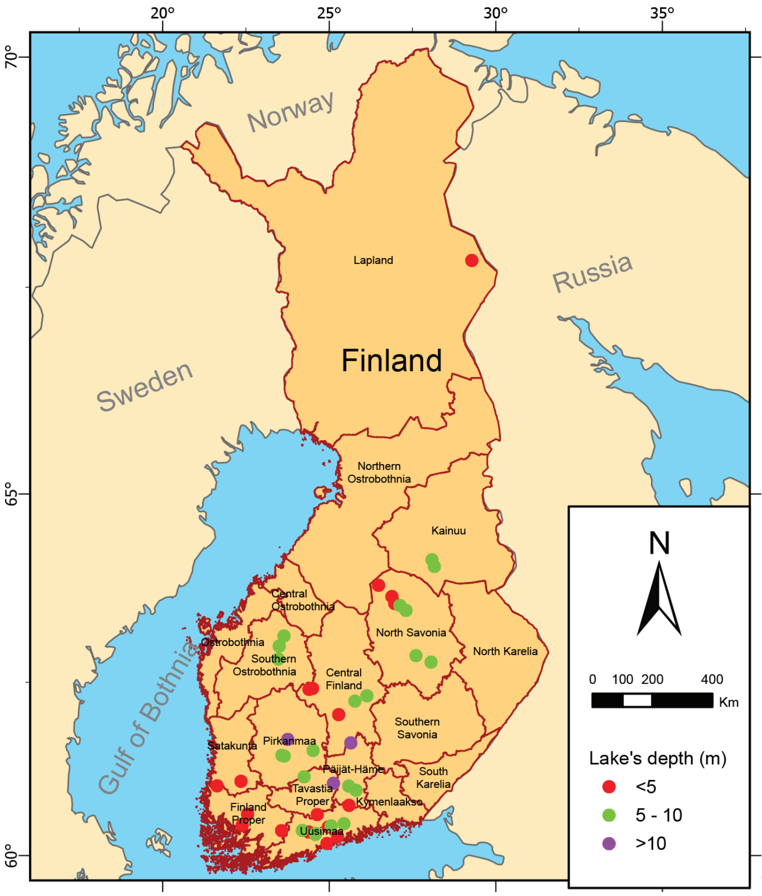

Fig 1. Geographical distribution of Finnish lakes studied for eutrophication based on the review.

ter coupling (George and Hurley 2002) that could affect the manifestation of eutrophication. Based on the information obtained from the publications, the study lakes were divided by summer mixing regime to polymictic vs. stratified (without defining whether the lakes were dimictic or meromictic), and by the surface area of the lakes to small vs. large lakes where < 10 km^2 were considered small following the criteria of Lehner and Döll (2004). Using the coordinates of the studied lakes, we depicted the distribution of these lakes using ArcGIS Pro (ver. 10.8.2). We then attempted to detect highlighted environmental changes corresponding to eutrophication in Finnish lakes as eutrophication indicators and assessed the extent to which they have been covered in related papers. Finally, different approaches to assessing these indicators in Finnish case studies are discussed in the following sections. For more information on the approaches and methods used to assess eutrophication (see Supplementary Information Table S1). The distribution and mean depth of the studied lakes are shown in Fig. 1, and more details, including the name, depth, surface area and summer mixing regime of the lakes, are provided in Supplementary Information Table S2.

Results

Case studies and their focus

The geographical scope of the articles varied between local and national studies, and global studies were discovered with Finnish cases included. Most studies in this review focused on lakes in the southern and central parts of Finland (Fig. 1). Based on the available data, the mean depth of 42% of the studied lakes was

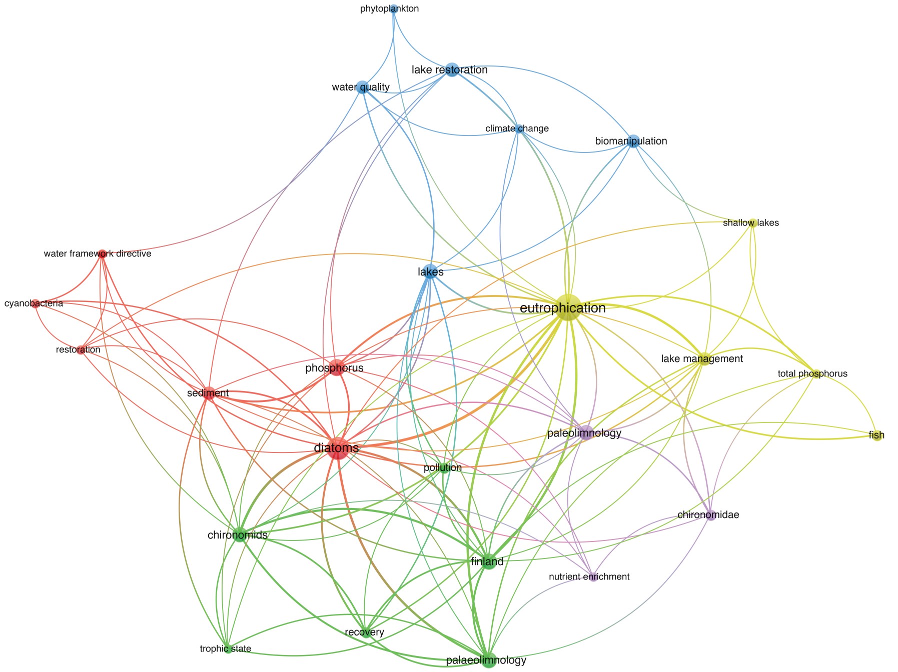

Fig 2. Bibliometric network of author keywords in the review.

less than 5 m, 51% had a mean depth between 5 and 10 m, and only 3% of the lakes had a mean depth of more than 10 m on average. In terms of mixing regime, 48% of the lakes experience stable summer stratification, while the rest are polymictic. In addition, 58% of the lakes have a surface area of less than 10 km^2, indicating that a vast number of studied eutrophic Finnish lakes are relatively small following the criteria determined by Lehner and Döll (2004).

Based on author keywords, the case studies reviewed were expectedly highly concentrated on eutrophication as the central term, whereas phosphorus (P), diatoms, sediment, chironomids, and paleolimnology were highlighted as the most repetitive in the network (Fig. 2). Author keywords thus suggest that a large focus of eutrophication studies in Finland has been on paleolimnological reconstructions spanning from preindustrial studies (Merilainen *et al.* 2003; Ventelä *et al.* 2016) to post 1950s displaying the signs of eutrophication (Kauppila *et al.* 2002; Luoto *et al.* 2017) and thus providing invaluable data on historical changes in lakes.

Although the keyword clusters were generated algorithmically, their thematic interpretation was based on the dominant keywords within each group. As several core concepts, such as phosphorus cycling and restoration, span multiple research areas, partial overlap among clusters reflects the interdisciplinary nature of eutrophication research rather than conceptual redundancy. In the red cluster, keywords in VOSviewer such as "sediment", "phosphorus", "diatoms", and "cyanobacteria" dominate other terms. This suggests that research on nutrient cycles, sediment deposition, and algal blooms is a key aspect of eutrophication. The green cluster highlights the importance of chironomids as bio-indicators of eutrophication in paleolimnological studies. The interconnection between "restoration", and terms like "biomanipulation", "phytoplankton" and "climate change" shows the key role of ecological restoration efforts in Finnish lakes and their interaction with climate change impacts. As expected, there has been a major focus on the P cycle in the water columns of lakes. In the yellow cluster the appearance

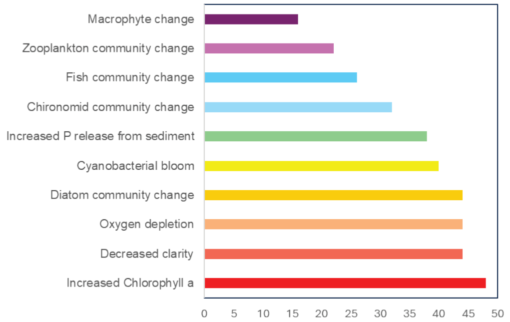

Fig 3. Eutrophication symptom coverage in publications (%).

of terms like "lake management", "total phosphorus", "shallow lakes", and "fish" in the same group, indicates the other aspects of eutrophication studies, namely ecological impacts of eutrophication and its management, especially in shallow lakes. The blue cluster represents the focus on restoration and management of lakes and the importance of biomanipulation and climate change effects in Finnish lakes. Overall, diverse groups with various aspects show the multidisciplinary nature of eutrophication assessment.

Indicators and symptoms of eutrophication

The common classification of trophic status is often based on concentration of Chl *a* and P, as well as water transparency (Carlson 1977). Oligotrophic lakes are characterized by low nutrient concentrations, low primary productivity, and high water transparency, whereas eutrophic lakes are typically distinguished by high nutrient availability, elevated algal biomass, and reduced transparency. Mesotrophic lakes represent an intermediate condition, with moderate nutrient concentrations, intermediate productivity, and partial reductions in water clarity (Wetzel 2001).

Signs of eutrophication have appeared or been studied in different ways across Finnish lakes (Fig. 3, Supplementary Information Table S3). Symptoms related to water quality changes, including decreased clarity, increased Chlorophyll *a* (Chl *a*), oxygen depletion, and increased sedimentary P have a great share of focus in the Finnish lake eutrophication literature. Consistent with the general understanding of the extensive role of internal P loading on lake eutrophication (Steinman and Spears 2020), a considerable number of lakes were suffering from internal P release from sediment, such as Kymijärvi, Littoistenjärvi and Iso-Kivijärvi (Kauppila *et al.* 2016; Sarvala *et al.* 2020; Silvonen *et al.* 2021).

The relative occurrence of eutrophication symptoms across Finnish lakes, classified by mixing regime and lake size, is shown in Fig 4. Cyanobacterial blooms, increased chlorophyll a, oxygen depletion, and decreased water clarity were reported considerably more frequently in polymictic lakes, whereas chironomid community changes were commonly reported in both polymictic and stratified lakes. Most other indicators also showed slightly higher occurrence in polymictic lakes, with the exception of fish and diatom community changes.

Regarding lake surface area, most of the indicators were more frequently reported in small lakes, especially cyanobacterial blooms, increased Chl a, and decreased clarity. Most other indicators showed a higher occurrence in small lakes, although the differences were generally modest, such as oxygen depletion, increased P from sediment, and community changes in fish, macrophytes, and zooplankton. But, diatom community change did not show a clear contrast between lake size classes.

Changes in the benthic community (e.g., diatoms and chironomids) and primary producers (e.g., cyanobacteria and macrophytes) were highlighted as other indicators of eutrophication. The diatom and chironomid communities and composition were addressed as the major elements in paleolimnological studies to reconstruct past lake water quality conditions. However, diatoms are more commonly assessed than chironomids. Additionally, fewer studies have focused on changes in fish and zooplankton communities than on other factors in the graph.

In the following sections, we describe the indicators and symptoms by which lake eutrophication has been assessed in the Finnish literature.

Phytoplankton communities

Phytoplankton community composition responds sensitively to changes in water quality, making

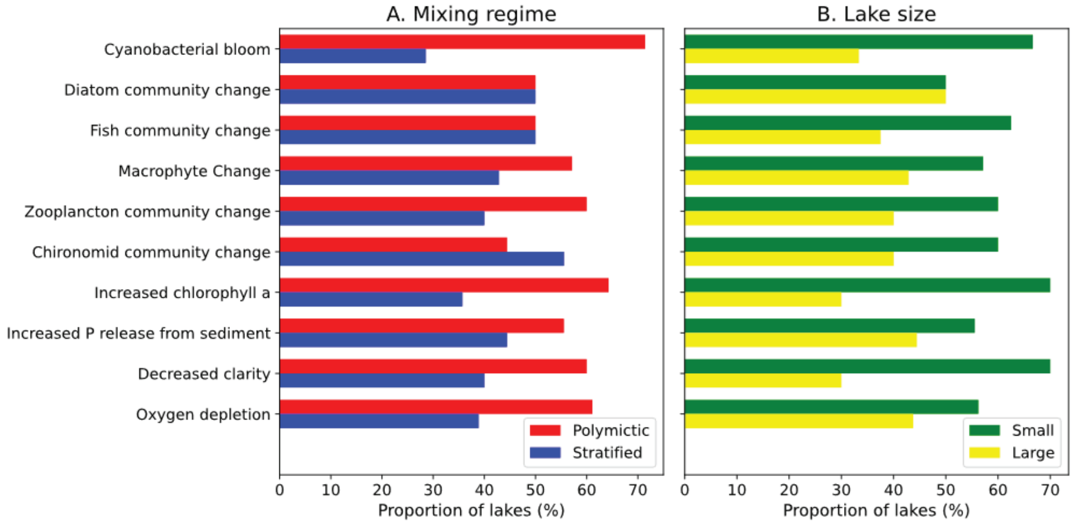

Fig 4. Distribution of Eutrophication symptoms across lakes by mixing regime and size.

phytoplankton a useful biological quality group for lake monitoring (Ptacnik *et al.* 2008). Changes in P and N concentrations are the main contributors to temporal declines in phytoplankton biomass and changes in community composition in Fennoscandian lakes (Paltsev *et al.* 2024). Indeed, the impacts of eutrophication on phytoplankton dynamics have been well addressed in Finnish case studies. For instance, Ptacnik *et al.* (2008) assessed the correlation between different phytoplankton groups, including chrysophytes, diatoms, and cyanobacteria, to Chl *a* and total phosphorus (TP). They explained that cyanobacteria may quickly respond to eutrophication, especially in low-alkaline lakes. Low alkaline conditions can be common in Scandinavian waterbodies, where igneous rock prevails over e.g., limestone and weathering products contributing to alkalinity are not released from the soil (Beldowski *et al.* 2010). Sarvala *et al.* (2020) explained that cyanobacteria were often dominant even at rather low TP levels (Around 40 µg L^{-1}). In Finnish lakes, cyanobacterial blooms are usually absent in lakes where epilimnetic TP levels are below 10 µg L^{-1}, but the probability of proliferation increases with increasing concentration (Vuorio *et al.* 2020).

The impact of human disturbance, including changes in land use, has led to more abundant cyanobacterial blooms in Finnish lakes, especially in late summer (Malve *et al.* 2007; Ruuhijärvi *et al.* 2010; Leppäranta *et al.* 2018; Sarvala *et al.* 2020; Silvonen *et al.* 2021). Furthermore, climate change and consequent implications for the duration of the growing season are mentioned as the probable drivers (Tammeorg *et al.* 2017; Zhao *et al.* 2024a). Subsequently, the duration of algal blooms in some Finnish lakes may have extended. For instance, in the lake Köyliönjärvi, SW Finland, the cyanobacterial occurrence recently can last for a month per late summer, as observed by Maeda *et al.* (2019) using remote sensing techniques.

In addition to resources, the impact of cascading trophic interactions, such as a change in zooplankton grazing pattern, affected by a change in fish predation, have been studied as potential drivers for increased cyanobacterial production (Rask *et al.* 2003; Malve *et al.* 2007; Ruuhijärvi *et al.* 2010; Taipale *et al.* 2020). Top-down control of phytoplankton by higher trophic levels is a well-known phenomenon in lakes (Carpenter *et al.* 1985; Vanni and Findlay 1990).

In addition to cyanobacteria, diatoms have been regarded as one of the key bioindicator communities in assessing how eutrophication progresses over time (Meriläinen *et al.* 2000, 2001; Kauppila *et al.* 2012; Luoto *et al.* 2017; Cantonati *et al.* 2020; Danesh *et al.* 2024). Diatoms are formed of silica, which is a resistant material, and preserved in sediment. They're utilized to reconstruct past environmental shifts in the lake ecosystem due to their sensitivity to nutrient availability, especially P. The diatom-based inferences provide important clues about nutrient levels and overall algal abundance during different climatic phases (Griffiths *et al.* 2022). For example, diatom analysis revealed that in glaciated, boreal environments, naturally eutrophic have been more common than previously thought (Kauppila *et al.* 2012; Shala *et al.* 2014; Tammelin *et al.* 2017; Tammelin and Kauppila 2018). It has also been useful to link trophic status shifts to different driving factors. For instance, Kauppila *et al.* (2002) linked two periods of slow and rapid eutrophication to intensified agriculture and municipal wastewater discharge, respectively. In addition to this, diatom analysis has been used to test if the proposed P reduction target is reasonable for the lakes or not (Tammelin *et al.* 2019). Weckström *et al.* (2015) studied diatom assemblage in lakes from Finland and China. They noticed the reflection of diatoms on the nutrient increase in both regions was similar despite the geographical difference.

There has been a valuable investigation on the correlation between phytoplankton communities and other factors during eutrophication, including lake depth, residence time, and the intensity of eutrophication and assessing the pattern of phytoplankton richness across latitude. For example, Tammelin and Kauppila (2018) noticed that due to higher nutrient turnover, phytoplankton changes were more noticeable in short-residence lakes. Also, eutrophication was more likely to occur in high drainage basin area-to-lake area ratios. According to another research from Cantonati *et al.* (2020), phytoplankton species richness was relatively higher at lower latitudes.

Benthic invertebrates

Zoobenthos, or interchangeably the benthic invertebrates, consisting of insect larvae (Chironomidae, Ephemeroptera, and Odonata), annelids, mollusca (bivalves and gastropods), macrocrustaceans (e.g., crabs), and benthic microcrustacea (e.g., Ostracoda) (Lurie 1998; Alford 2012; Gibb and Oseto 2020; Silvonen *et al.* 2023). Benthic invertebrates populate bottom sediments or the surface and substrates above it. Like other higher trophic levels, zoobenthos can regulate the type and quantity of phytoplankton, zooplankton, connected algae, and aquatic plants in lakes. This regulation occurs primarily through indirect pathways, such as bioturbation, nutrient recycling, and modification of sediment–water nutrient fluxes, rather than through direct grazing (Nevalainen and Luoto 2013; Luoto *et al.* 2019). In contrast, direct regulation of pelagic phytoplankton biomass is mainly exerted by zooplankton (Lampert and Sommer 2007). Benthic invertebrate activity regulates the flow of nutrients and toxins between the sediment-water interface (Strayer 2009; Leslie and Lamp 2019).

Benthic invertebrates are sensitive to climate change and closely linked to the variation of organic matter sedimentation, making them useful in determining the timing and extent of eutrophication, particularly if there is a lack of long-term limnological data (Meriläinen *et al.* 2000; Griffiths *et al.* 2024). Indeed, zoobenthos have been categorized into functional groups according to their sensitivity to factors like oxygen requirements, organic matter sedimentation, and aquatic macrophyte abundance (Itkonen *et al.* 1999; Shala *et al.* 2014; Luoto *et al.* 2017; Griffiths *et al.* 2021), which are key factors in eutrophication. In some paleolimnological studies, zoobenthos were even better reflectors of intensified human pollution in boreal lakes than diatoms (Hynynen *et al.* 2004; Luoto *et al.* 2017).

Among different groups of zoobenthos, chironomids are one of the most common bio-indicators, which have been assessed to reconstruct the history of nutrient dynamics in waterbodies and track eutrophication in Finnish case studies. Their wide distribution, sensitivity to oxygen availability, ease of identification, and variation in different nutritional conditions are some crucial reasons why they have been analyzed to represent different trophic status in different boreal lakes (Itkonen *et al.* 1999; Meriläinen *et al.* 2001; Brodersen and Quinlan 2006; Vesterinen *et al.* 2022). The other zoobenthos group sensitive to eutrophication is Annelid with *Lim-*

nodrilus hoffmeisteri as an example adopted to low oxygen conditions during eutrophication (Jyväsjärvi *et al.* 2013). Another example is oval epibenthos, which increased up to 30% during eutrophic and hypereutrophic periods, according to the analysis of sediment core taken from Tiiläänjärvi (Nevalainen and Luoto 2017).

Fish

The relationship between the change in fish communities and water quality degradation due to eutrophication is another aspect of eutrophication assessment that has been widely addressed. The dominance of roach (*Rutilus rutilus*) and other cyprinids, such as the bronze bream (*Abramis brama*) and silver bream (*Blicca bjoerkna*) in Finnish lakes have coincided with eutrophic conditions (Lappalainen *et al.* 2000, 2005; Karels and Niemi 2002; Uusitalo *et al.* 2018) consistent with the general assumption of cyprinids being the dominant fish group in eutrophic lakes (Jeppesen *et al.* 2000; Olin *et al.* 2002). In addition, the decline in sensitive species like whitefish (*Coregonus lavaretus*), Eurasian minnow (*Phoxinus phoxinus*) and the European perch (*Perca fluviatilis*) coincides with elevated nutrient concentrations (Karels and Niemi 2002; Nevalainen *et al.* 2011). Changes in fish community structure may greatly affect phytoplankton communities via cascading trophic interactions (Carpenter *et al.* 1985). The increasing abundance of zooplanktivorous and benthivorous fishes poses a risk for water quality not only via top-down but also via bottom-up control, i.e. by maintaining internal P loading through bioturbation (Søndergaard *et al.* 2008). Hence, the fish community structure can be an important indicator of the state of foodweb and lake eutrophication dynamics in general.

Zooplankton

Zooplankton have been considerably assessed during eutrophication in different Finnish lakes as they play a key role in controlling phytoplankton communities (Supplementary Information Table S2).

The variation of zooplankton biomass can be affected by many elements, particularly nutrient availability and fish (Nevalainen and Luoto 2013). Long-term monitoring of water quality in some Finnish lakes highlighted the sensitivity of zooplankton to nutrient enrichment (Sarvala *et al.* 2000; Malve *et al.* 2007; Nevalainen and Luoto 2017). For instance, (Nevalainen and Luoto 2017) explained how small-bodied filter-feeding zooplankton such as *Bosmina* sp. became more dominant in response to increased nutrients in lakes Mallusjärvi (Orimattila) and Tiiläänjärvi (Askola). The other example of zooplankton response to water quality change can be seen in lakes Äimäjärvi and Vesijärvi, where crustacean zooplankton, namely *Daphnia* sp. increased as a response to biomanipulation (Sarvala *et al.* 2000). Lake Kirkkojärvi, in turn, experienced a rise in zooplankton biomass during the eutrophication period and followed a steep decline when chemical precipitation took place (Sarvala and Helminen 2023). In lake Pyhäjärvi, zooplankton grazing was more effective in controlling nitrogen-fixing cyanobacteria than TP concentration (Malve *et al.* 2007). However, zooplankton communities are sensitive to predation exerted by fishes, which may on the other hand impact the indicator value but also provide information on the structure of foodweb. Changes in fish community structure can significantly affect zooplankton community composition. For instance, Ventelä *et al.* (2011) demonstrated that the zooplankton population was indirectly impacted by ice-cover duration, because the ice-seine fishing pressure on vendace was reduced due to a shorter ice-on period, consequently leading to a major decline in the crustacean zooplankton population, namely *Daphnia* sp. and *Bosmina* sp.

Macrophytes

Macrophyte community change has been another symptom of eutrophication in Finnish case studies. The abundance and cover of aquatic vegetation have been measured by e.g., conducting boat surveys or diver-assisted observations along transects, and in some cases sampling by raking (Sarvala *et al.* 2020; Suhonen 2021). The number of macrophyte-associated taxa and the macrophyte abundance index have also been used to reconstruct historical macrophyte variation during a specific period (Ventelä *et al.* 2016). Changes in the abundance of aquatic macrophyte species have been correlated to the rising trend of eutrophication in Finnish waterbodies (Ventelä *et al.* 2016; Suhonen 2021). Clear-water phases have coincided with a balanced macrophyte cover without excessive overgrowth or undergrowth, bringing a stable ecosystem with a more piscivorous fish population (Ruuhijärvi *et al.* 2010). Submerged macrophytes are especially important in shallow lakes, in which they can greatly contribute to the stability of clear-water equilibria (Scheffer *et al.* 1993; Søndergaard *et al.* 2008; Triest *et al.* 2016; Sarvala *et al.* 2020). The suppression of phytoplankton by submerged macrophytes can be promoted by, for example, resource competition, zooplankton habitat provision, suppression of sediment resuspension, and excretion of allelopathic substances (Scheffer *et al.* 1993; Vermaat *et al.* 2000; Hupfer and Dollan 2003; Mulderij *et al.* 2007). However, both dieback and overgrowth of macrophytes are conditions that can impact the trophic status but also the recreational value of lakes. As evidence of this, overgrowth of invasive *Elodea canadensis* due to eutrophication was followed by a collapse in following years in lake Littoistenjärvi, leading to hypereutrophic condition (Sarvala *et al.* 2020).

Water quality

Water quality parameters have been regarded as the key elements to assess eutrophication in most studies of freshwater lakes, especially P, which is mostly considered the limiting factor of eutrophication (Wang *et al.* 2024). Phosphorus often also limits the primary production in Finnish lakes rather than nitrogen (N) (Pietiläinen and Räike 1999). Consequently, most focus in Finnish nutrient-related studies has plausibly been on P dynamics and elements that can affect this cycle (e.g., oxygen, turbidity, water temperature) (Laakso *et al.* 2023; Zhao *et al.* 2024b, a).

Oxygen depletion is a common eutrophication-related problem in Finnish lakes and in the northern hemisphere in general (Jansen *et al.* 2024). It subsequently promotes internal loading of P and poses negative consequences for biota. For instance, under-ice fish kills are a common phenomenon in eutrophic lakes with potential cascading impacts to lower trophic levels (Ruuhijärvi *et al.* 2010). In e.g., lake Äimäjärvi, anoxia-induced fish kill led to decreased water transparency and increased microbial decomposition of organic matter (Ruuhijärvi *et al.* 2010). Additionally, under-ice anoxia can impact the survival of other biota, including macrophytes. In Lake Littoistenjärvi, for instance, winter anoxia has resulted mass mortality of *Elodea canadensis*, followed by increased P and Chl *a* concentration during summer in 1999 (Sarvala *et al.* 2020). Following this, increased turbidity due to proliferation of phytoplankton blooms prevented submerged macrophytes from recolonizing (Sarvala *et al.* 2020).

A peculiarity in Finnish and boreal lakes in general is the often naturally high organic carbon (OC) content (Kortelainen and Mannio 1990) that shapes the lacustrine light climate and mixing regimes (Hongve 2002; Hakala 2004; Thrane *et al.* 2014) with consequent implications for vertical gradients of dissolved oxygen and other substances (Couture *et al.* 2015) Increasing concentration of OC, i.e. browning, has been widely reported in Finnish lakes during the recent decades (Räike *et al.* 2024). Eutrophication studies evaluated in this review did not cover the symptoms of browning but we highlight potential interactions of OC with nutrients that may alter the responses of lakes to eutrophication via OC-induced changes in the physical, chemical and biological properties of aquatic ecosystems (Solomon *et al.* 2015; Creed *et al.* 2018; Blanchet *et al.* 2022).

Sediment

Sediment plays a crucial role in regulating lake water quality by acting both as a sink and a source of nutrients, particularly P (Kauppila *et al.* 2002). Understanding the P dynamics in different depths of a lake, from sediments to the surface layer, under different processes and conditions has been a major factor in assessing eutrophication also in Finnish studies. These processes include climate change, remineralization, biological change (e.g., shifts in species composition or microbial activity), and restoration activities in past, present, and future scenarios (Voutilainen and Huuskonen 2010; Nürnberg *et al.* 2012; Anttila *et al.* 2013; Zhao *et al.* 2024a). Despite this, sediment nutrients are ignored in the ecological status assessment of lakes (Horppila 2019).

According to the literature, continuous internal loading due to sediment P release is a big concern across Finnish waterbodies (Niinioja *et al.* 2003; Miettinen *et al.* 2005; Nevalainen *et al.* 2011; Jilbert *et al.* 2020). In cases where internal nutrient loading contribution is considerable (e.g., Lake Kymijärvi) the significant amounts of sedimentary P release occur during anoxic periods (Silvonen *et al.* 2021). However, Tammeorg *et al.* (2017) explained that in mesotrophic lakes internal P from an oxic layer of sediment can be more intensive than anoxic one, especially in shallower areas, suggesting a limitation of aeration in the studied cases.

The binding capacity of P to iron (Fe), manganese (Mn), and humic substances are other aspects that have been extensively evaluated in recent studies (Jilbert *et al.* 2020; Tammeorg *et al.* 2022; Laakso *et al.* 2024; Zhao *et al.* 2024a). Laakso *et al.* (2023) demonstrated that iron capacity in blocking P in Lake Köyliönjärvi can account for 40–50% of the total sediment. On the other hand, some recent studies revealed that even in Fe-rich and Mn-rich lakes, where P burial is expected to be relatively efficient, sedimentary P release to the water column can continue to a large extent (Jilbert *et al.* 2020; de Toledo and Baulch 2023; Zhao *et al.* 2024a).

The rate of organic matter (OM) remineralization is the other factor addressed in recent studies. For instance, it is said that in shallow lakes P diffuses more quickly because higher temperatures speed up the breakdown of OM, especially its algae-derived autochthonous component (Tammeorg *et al.* 2017; Zhao *et al.* 2024a). Supporting this idea, the long-term monitoring of Lake Säkylän Pyhäjärvi showed higher sedimentary P release in warm years in comparison with lower external P (Nürnberg *et al.* 2012).

The remineralization rate of OM, which is sensitive to climate warming, has been used to explain the disconnection between P and cyanobacteria in other case studies, where the opposite trend is observed between P concentration and cyanobacterial blooms (Paterson *et al.* 2017; Favot *et al.* 2019). Differences in shallowness and the remineralization of organic matter are mentioned as the main contributing factors to differences in P content at different points of a lake (Valpola *et al.* 2007; Vuorio *et al.* 2020).

Discussion

Alignment of assessed bio-indicators with WFD monitoring activities

According to the review results, phosphorus, diatoms, sediment, chironomids, and paleolimnology were highlighted as the most intensively studied aspects in Finnish eutrophication-related studies. Additionally, the BQEs phytoplankton, benthic invertebrates, macrophytes, and fish, following WFD monitoring activities (van Puijenbroek *et al.* 2015) were frequently addressed, expectedly.

The use of biological indicators has proven to be effective in understanding historical and contemporary variation in water bodies that can assist in setting the targets of restoration attempts. Multiple-proxy analyses, which involve combining biological and environmental proxies, is suggested as a trusting approach in most studies to follow eutrophication footprint in past decades (Meriläinen *et al.* 2000, 2001; Kauppila and Valpola 2003; Langdon *et al.* 2006; Brodersen and Quinlan 2006; Luoto *et al.* 2017; Griffiths *et al.* 2024; Litmanen *et al.* 2024). In paleolimnological studies, the links between chironomid and diatom assemblages with changes in nutrient levels, temperature, and oxygen saturation, make these organismal groups reliable bioindicators of eutrophication, especially in lakes where a lack of observational data is the main challenge to reconstruct historical changes of water quality. According to these studies, prior to major industrialization, Finnish lakes had low nutrient levels followed by accelerated eutrophication after the 1950s associated with agricultural intensification and urban development. Due to substantial loading of domestic and industrial wastewaters, several studies demonstrate severe eutrophication of lakes in mid-1900s (Horppila *et al.* 2017; Salonen *et al.* 2020; Sarvala *et al.* 2020). However, in cases restoration practices in recent decades following improved wastewater treatment and nutrient management have succeeded to reduce the nutrient concentrations and alleviate the symptoms of eutrophication (Kauppila and Valpola 2003; Ventelä *et al.* 2016; Salminen *et al.* 2021).

Future studies could consider approaches that can offer distinct insights into the nutrient dynamics of aquatic ecosystems, enhance the accuracy of reconstructions and improve the predictive capability of ecological models. It is said that in analyzing bioindicators, considering both epilimnetic and hypolimnetic systems is essential (Hynynen *et al.* 2004; Luoto *et al.* 2017). The potential of bioindicator-based models to predict eutrophication trends under varying climate change scenarios, including lakes with diverse trophic statuses in diatom/chironomid-inferred models, should be investigated. Doing long-term monitoring programs instead of short-term ones have been emphasized to analyze gradual ecological shifts and provide observational data for forecasting future changes in a more accurate way (Meriläinen *et al.* 2000; Griffiths *et al.* 2024; Danesh *et al.* 2024).

Further research into functional groups of biological indicators and their role in nutrient cycling under environmental stressors can further enhance our understanding of lake ecosystems (Griffiths *et al.* 2024; Danesh *et al.* 2024). Furthermore, considering additional elements of aquatic life that contribute to the nutrient cycle between water and sediment is suggested (Sarvala *et al.* 2000; Kauppila *et al.* 2012; Marzecová *et al.* 2017; Kokkonen *et al.* 2019). Zooplankton showed considerable sensitivity to climate change, nutrient concentration change, and fish predation in Finnish lakes. Hence, we side with Jeppesen *et al.* (2011) stating that zooplankton would be a relevant indicator of eutrophication to be added in WFD monitoring activities.

Lake morphometry shaping eutrophication responses

Assessing the distribution of eutrophication indicators across different summer mixing regime and area of studied Finnish lakes highlighted the importance of morphometric characteristics in eutrophication assessment.

The review showed that water quality indicators and sedimentary nutrient release were more dominant in polymictic mixing regime which happen in shallower and smaller lakes. In shallower water bodies wind-driven sediment resuspension is the major driver of internal nutrient loading, followed by considerable unpleasant consequences, such as oxygen depletion, decreased clarity of water, and cyanobacterial bloom (Zhao *et al.* 2024b). In contrast, stratification in deep lakes enhance the chance of nutrient burial. Additionally, larger lakes had less eutrophication symptoms, maybe because large lakes usually have relatively higher inflow and shorter hydraulic residence time than the small ones (George and Hurley 2002; Hendriks *et al.* 2012). Higher inflow shortens residence time, enhancing export and dilution of nutrients, which suppresses eutrophication, the opposite of stagnant, long-residence systems where nutrients accumulate and result in algal blooms (Zhao *et al.* 2022)..

Perspectives for restoration activities

One of the main concerns before implementing any restoration strategy is whether we have a comprehensive picture of nutrient cycling or not. P has been regarded as the limiting factor of eutrophication in most waterbodies (Sarvala *et al.* 2020; Vuorio *et al.* 2020; Laakso *et al.* 2024) and controlling its cycle is necessary in restoration efforts. However, an increasing number of studies have highlighted the importance of N in controlling eutrophication dynamics in lakes (e.g., González Sagrario *et al.* 2005; Paerl *et al.* 2016; Hellweger *et al.* 2022) and the need for integrating N in nutrient control has been increasingly recognized (e.g., Maberly *et al.* 2020). There are several experiences where restoration efforts were unable to improve the water quality of lakes globally (Søndergaard *et al.* 2007; Gao and Zhang 2010; Brettschneider *et al.* 2023). Consequently, there is still a need to better understand the relationships between different factors affecting the nutrient cycle, such as ecozone characteristics, soil types, oxygen saturation levels, sediment P-binding capabilities, water depth, remineralization of organic matter, weather and wind conditions, and the spatial and temporal differences of P and N limitation in lakes (Jilbert *et al.* 2020; de Toledo and Baulch 2023; Zhao *et al.* 2024a). Lack of attention to these factors and their role in eutrophication may lead to inefficiency of restoration efforts, especially those suffering from intensive internal pollution. For example, wind disturbance, water temperature change, and short-term weather change (e.g., change of ice-out dates) can indirectly impact on the nutrient cycle (Favot *et al.* 2019), while sediment release and external loading can directly exacerbate the trophic status of a water body (Horppila *et al.* 2019; Sarvala *et al.* 2020). Accordingly, studying correlations of different forms of P, such as TP, soluble reactive P, and inorganic P in anoxia with other above-mentioned factors is strongly recommended (Tammeorg *et al.* 2017; Laird *et al.* 2020; Zhao *et al.* 2024a).

One of the most important things that can help us choose better strategies for the recovery of a lake is studying the past condition of a lake and the lake's response to past anthropogenic activities or natural shifts. More specifically, assessing the correlation between changes in nutrient dynamics and environmental shifts can guide us to make more informed decisions about restoration plans. The results of recent studies highlight the need to rethink traditional beliefs and try to have a more comprehensive picture of the nutrient dynamics in a lake system before beginning any actions against eutrophication in practice. Only focusing on a few elements controlling this circulation can deceive us to provide a wise strategy to control water quality depletion (Tammeorg *et al.* 2017). Subsequently, each restoration activity should be based on a system analysis defining the stressors involved together with the targets and appropriate measures ensuring sustainable lake restoration (e.g., Lürling *et al*. 2016; Tammeorg *et al.* 2024).

Restoring eutrophic lakes has been challenging and, in some cases, unsuccessful to reach the determined targets, so there is need to reevaluate strategies for mitigation efforts (Luoto *et al.* 2017; Vuorio *et al.* 2020). In shallow lakes especially, effectiveness of single restoration efforts can be hampered with nonlinear response trajectories mediated by interactions with biota (Scheffer *et al.* 1993; Jeppesen *et al.* 2012; Sarvala *et al.* 2020). Sustainable, longer-term response of a lake to restoration requires re-establishment of such in-lake processes that stabilize water quality and ecological diversity (Moss 1990; Scheffer *et al.* 1993). In most cases, combined measures targeting multiple processes are needed to break down a eutrophied state (Jing *et al.* 2019). Indeed, the review showed that different forms of internal P loading driven by physical disturbance (resuspension, bioturbation) or P diffusion due to e.g., anoxic conditions may have different shares in water column TP, emphasizing the need to match restoration practices to the main drivers of internal P loads. Prioritizing the zones having more share in eutrophication (like shallower areas of lakes) (Valpola *et al.* 2007; Jyväsjärvi *et al.* 2013; Zhao *et al.* 2024a) and understanding the balance between permanent burial of P and external P loading to assessing the timescale of recovery (Jilbert *et al.* 2020) are to be considered in management of eutrophication in boreal lakes.

Management strategies should not only focus on reducing one specific nutrient, without assessing other contributing factors (sediment, biota) to nutrient enrichment (Valpola *et al.* 2007; Kosten *et al.* 2009; Paterson *et al.* 2017; Vuorio *et al.* 2020). They should be more targeted and effective and must be integrated with a broader understanding of how various environmental factors affect nutrient cycling. Allocating a longer timeframe for mitigation practices to avoid failure in recovery practices is highly recommended (Rask *et al.* 2003; Nürnberg *et al.* 2012; Jyväsjärvi *et al.* 2013). A fundamental prerequisite for lake restoration is also managing the external loading in tolerable boundaries.

Conclusions

In this review, we assessed how different indicators contribute to a better understanding of the historical and current condition of lakes affected by eutrophication using Finnish case studies as an example. In regards of water quality, most studies had expectedly focused on P dynamics in lakes. However, with the increasing understanding on the importance of N in shaping eutrophication dynamics in lakes, we highlight the need for keeping both nutrients as indicators in future eutrophication assessments and encourage future studies to assess means for mitigating N in addition to P. Additionally, with the observed increasing trends of OC in Boreal lakes and its versatile impacts on physical and chemical properties of lakes and their biological communities, the role of OC in eutrophication-related studies should not be neglected. From the BQEs, implications of eutrophication for diatoms and phytoplankton were most frequently covered by the reviewed literature while the changes in fish, benthic invertebrate and macrophyte communities were less frequently studied. Monitoring of lakes on broad, long-term scales often falls short due to low sampling frequency and resolution due to limitations in for instance financing (Tammeorg *et al.* 2025). However, with versatile implications of eutrophication to biological communities in lakes depending on their initial characteristics, our review underscores the importance of exploring all possible eutrophication metrics from biological to water quality parameters in-depth to allow for reliably assessing the ecological status of lakes, in addition to determining possible restoration targets and evaluating success of restoration programs. From the biological indicators included in this study, zooplankton is the only group not systematically included in WFD monitoring activities. However, numerous studies included in the review supported the conclusion of Jeppesen *et al.* (2011) that this biological indicator would be useful in assessing lake ecosystem dynamics and allowing for detection of changes in lake nutrient and foodweb dynamics both at the present time and historically from paleolimnological reconstructions. Highlighting the importance of sediments in not only describing the past and present conditions of a lake but also shaping and controlling eutrophication dynamics in lakes, a vast proportion of reviewed studies had focused on internal nutrient loading. This is in concordance with Horppila (2019) who advocated inclusion of sediment nutrients in ecological status assessment in order to better allow for assessing the potential timescales needed for the recovery of lakes from past loading. The need for a more holistic approach is emphasized to have a more comprehensive strategy towards managing lakes. To achieve this, future studies should focus on integrating a variety of environmental and biological proxies to assess the eutrophication process, before and after recovery solutions. This will help decision-makers to have a clearer picture of the effectiveness of restoration efforts in future scenarios where implications of climate change add a lot of complexity to the eutrophication process.

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