Dissolved, Transformed, Retained

Carbon Cycling in Freshwater and Coastal Systems

Jones, Kevin

2025

Document Version:
Publisher's PDF, also known as Version of record

Link to publication

Citation for published version (APA):
Jones, K. (2025). *Dissolved, Transformed, Retained: Carbon Cycling in Freshwater and Coastal Systems*. Lund University (Media-Tryck).

Total number of authors:
1

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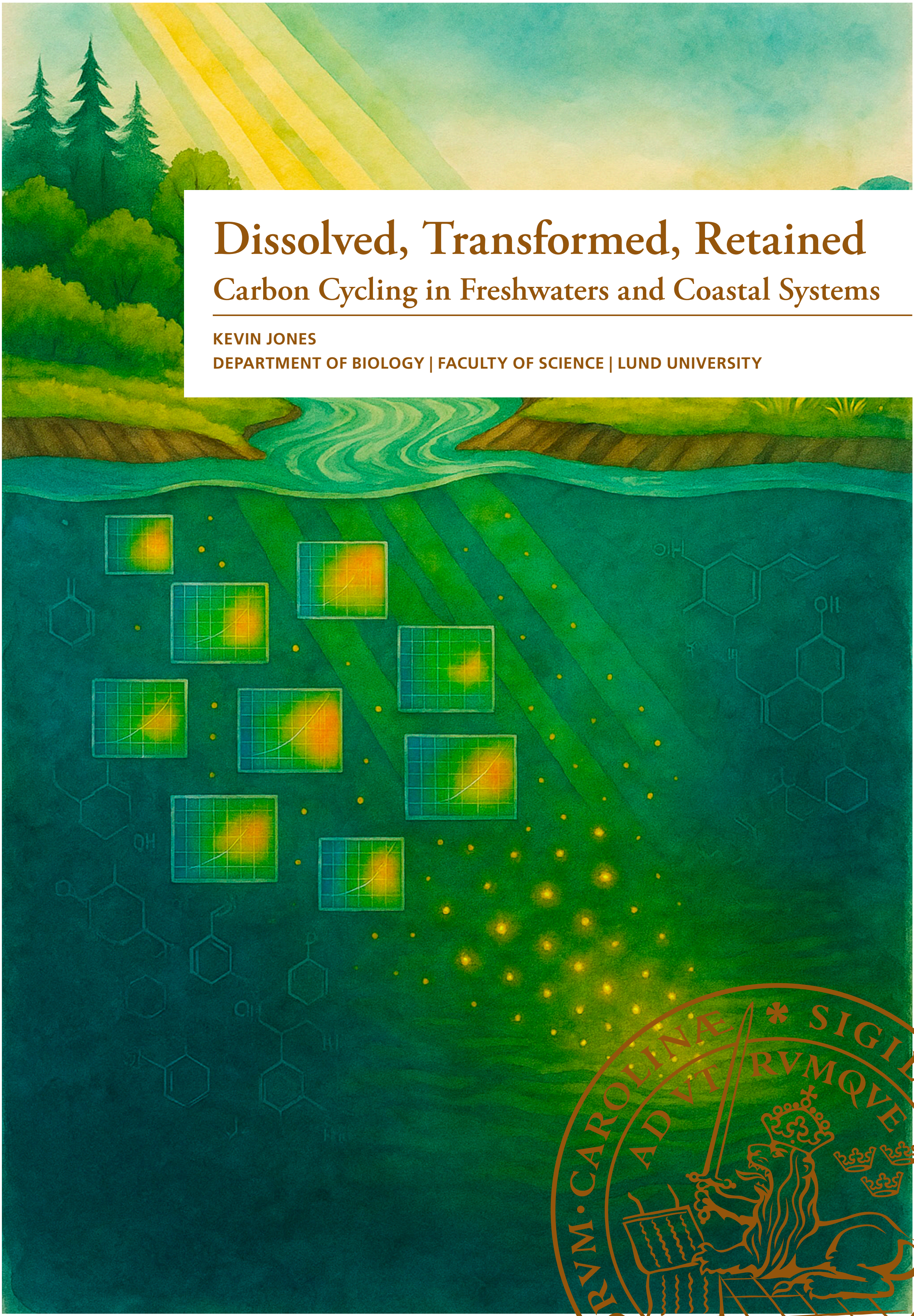
DEPARTMENT OF BIOLOGY | FACULTY OF SCIENCE | LUND UNIVERSITY



Dissolved, Transformed, Retained

Carbon Cycling in Freshwaters and Coastal Systems

Kevin Jones

DOCTORAL DISSERTATION

Doctoral dissertation for the degree of Doctor of Philosophy (PhD) at the Faculty of Science at Lund University to be publicly defended on the 14th of November at 09.00 in the Blue Hall, Department of Biology, Ecology Building, Sölvegatan 37 Lund

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Organization: LUND UNIVERSITY

Document name: Doctoral Dissertation

Date of issue: 14 Nov 2025

Author(s): Kevin Jones

Sponsoring organization:

Title and subtitle: Dissolved, Transformed, Retained: Carbon Cycling in Freshwaters and Coastal Systems

Abstract:

Freshwater ecosystems in boreal and temperate regions are undergoing rapid change as increasing inputs of terrestrially derived dissolved organic matter (DOM) and nutrient enrichment alter ecosystem functioning. These processes, known as brownification and eutrophication, vary across space and time but can profoundly reshape carbon cycling, microbial activity, and water quality. This thesis investigates how seasonal variability, nutrient availability, and wetland design interact to influence DOM transformations in freshwater and coastal systems.

Field studies and experimental manipulations demonstrate that pulses of terrestrial DOM during high-flow events and seasonal transitions strongly affect DOM composition and microbial bioavailability. Nutrient enrichment stimulates microbial uptake but lowers bacterial growth efficiency, shifting carbon use toward respiration and CO_2 release rather than biomass production. Sunlight also plays a critical role: photochemical processes fragment aromatic DOM into smaller, more labile compounds, particularly in shallow, well-lit waters where exposure is prolonged. The relative importance of microbial versus photochemical pathways shifts with season, with warmer nutrient-rich periods amplifying microbial respiration and clearer shallow systems enhancing photodegradation. Constructed wetlands provide an opportunity to harness these processes for management. Results show that both water depth and seasonal light regimes determine whether DOM removal is dominated by microbial reworking or photochemical breakdown. Shallow wetlands promote rapid photodegradation, while deeper systems sustain microbial transformations that further process DOM before it leaves the wetland.

Overall, this thesis demonstrates that the fate of DOM in freshwaters is shaped by the combined effects of light, nutrients, hydrology, and wetland design. By linking natural seasonal variability with targeted wetland manipulations, it provides new insights into how freshwater carbon cycling may respond to environmental change and highlights how strategically designed wetlands can mitigate brownification across seasons.

Key words: Dissolved organic matter (DOM), brownification, eutrophication, microbial carbon cycling, photodegradation, constructed wetlands, seasonal variability, aquatic biogeochemistry

Language: English

Number of pages: 68

ISSN and key title:

ISBN: 978-91-8104-701-1 (print), 978-91-8104-702-8 (electronic)

Signature

Date 2025-10-01

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In text photo (Figure 6, p.33) by Jasmine Borget
Cover image by Kevin Jones
All other figures, tables, and pictures are by Kevin Jones

Faculty of Science
Department of Biology

ISBN 978-91-8104-701-1 (print)
ISBN 978-91-8104-702-8 (electronic)

Printed in Sweden by Media-Tryck, Lund University,
Lund, 2025

The Scars of Man on the Once Nameless Wilderness

- Austin Lunn (Panopticon), 2018

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Paper II

Jones, K., Liess, A., & Sjöstedt, J. (2024). Microbial carbon utilization in a boreal lake under the combined pressures of brownification and eutrophication: insights from a field experiment. *Hydrobiologia*. https://doi.org/10.1007/s10750-024-05718-9

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Author Contributions

I. Conceptualization, Methodology, Investigation, Data curation, Formal analysis, and Visualization were carried out by KJ and JS. Writing - original draft was performed by KJ, while Writing - review & editing was conducted by KJ, JS, and MB. Supervision and Funding acquisition were provided by JS.

II. Conceptualization, Methodology, Investigation, Data curation, and Formal analysis were conducted by KJ, JS, and AL. Visualization was carried out by KJ. Writing - original draft was prepared by KJ; while Writing - review & editing was performed by KJ, JS, and AL. Supervision and Funding acquisition were provided by JS.

III. Conceptualization was carried out by SL, JN, SB, JS, and KJ. Methodology and Project administration, including mesocosm coordination and preparation, were performed by SL, JN, and SB. Investigation and Data curation were conducted by all authors, with significant contributions to sample analysis and data generation from KJ and JS. Formal analysis and Visualization were conducted by KJ. Writing - original draft was prepared by KJ, and Writing - review & editing was performed by all authors. Supervision and Funding acquisition were provided by JS.

IV. Conceptualization and Methodology were conducted by KJ, AL, and JS. Investigation and Data curation were performed by all authors. Formal analysis and Visualization were carried out by KJ and JS. Writing - original draft was prepared by KJ, while Writing - review & editing was performed by all authors. Supervision and Funding acquisition were provided by JS.

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Publications not contained in this thesis

Borgert, J., Jones, K., Nilsson, J. E., Sjöstedt, J., & Liess, A. (2025). Seasonal Dynamics of Brownification Mitigation in Constructed Wetlands. *Wetlands*, *45*(5), 63. https://doi.org/10.1007/s13157-025-01944-6

Pedregal-Montes, A., Jennings, E., Kothawala, D., Jones, K., Sjöstedt, J., Langenheder, S., Marcé, R., & Farré, M. J. (2024). Disinfection by-product formation potential in response to variability in dissolved organic matter and nutrient inputs: Insights from a mesocosm study. *Water research*, *258*, 121791. https://doi.org/https://doi.org/10.1016/j.watres.2024.121791

Abbreviations

DOM	Dissolved Organic Matter
CDOM	Chromophoric Dissolved Organic Matter
FDOM	Fluorescent Dissolved Organic Matter
EEM	Excitation–Emission Matrix
PARAFAC	Parallel Factor Analysis
SR	Slope Ratio (S275–295 / S350–400)
BP	Bacterial Production
BR	Bacterial Respiration
BOD	Biological Oxygen Demand
DO	Dissolved Oxygen
BGE	Bacterial Growth Efficiency
DOC	Dissolved Organic Carbon
SUVA	Specific Ultraviolet Absorbance (at 254 nm, SUVA254)
CW	Constructed Wetland
TOC	Total Organic Carbon
UV-VIS	Ultraviolet–Visible (Spectroscopy)

Abstract

Freshwater ecosystems in boreal and temperate regions are undergoing rapid change as increasing inputs of terrestrially derived dissolved organic matter (DOM) and nutrient enrichment alter ecosystem functioning. These processes, known as brownification and eutrophication, vary across space and time but can profoundly reshape carbon cycling, microbial activity, and water quality. This thesis investigates how seasonal variability, nutrient availability, and wetland design interact to influence DOM transformations in freshwater and coastal systems.

Field studies and experimental manipulations demonstrate that pulses of terrestrial DOM during high-flow events and seasonal transitions strongly affect DOM composition and microbial bioavailability. Nutrient enrichment stimulates microbial uptake but lowers bacterial growth efficiency, shifting carbon use toward respiration and CO_2 release rather than biomass production. Sunlight also plays a critical role: photochemical processes fragment aromatic DOM into smaller, more labile compounds, particularly in shallow, well-lit waters where exposure is prolonged. The relative importance of microbial versus photochemical pathways shifts with season, with warmer nutrient-rich periods amplifying microbial respiration and clearer shallow systems enhancing photodegradation. Constructed wetlands provide an opportunity to harness these processes for management. Results show that both water depth and seasonal light regimes determine whether DOM removal is dominated by microbial reworking or photochemical breakdown. Shallow wetlands promote rapid photodegradation, while deeper systems sustain microbial transformations that further process DOM before it leaves the wetland.

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Popular Science Summary

Many of us have noticed that lakes, rivers, and coastal waters are becoming darker. This "brownification" is caused by increasing amounts of dissolved organic matter (DOM), which is mainly organic carbon leaching from soils and vegetation. Brown water is more than just a visual change: it reduces water clarity, alters food webs, fuels microbial respiration, and can increase greenhouse gas emissions from inland waters. At the same time, many aquatic systems also face nutrient enrichment from agriculture, forestry, and other human activities. Understanding how carbon and nutrients interact in freshwaters is essential for predicting future water quality and developing ways to protect aquatic ecosystems.

In my research, I studied how the quantity and quality of DOM change with seasons and across landscapes, and how microbes respond when DOM and nutrients are supplied together. By combining field studies in rivers and lakes with controlled mesocosm experiments, I was able to explore both natural variability and specific experimental manipulations. The results show that DOM exported during spring and autumn rains is especially bioavailable, which means it is quickly consumed by microbes and drives oxygen demand. Agricultural catchments contribute more labile DOM, while forested catchments export larger but more resistant DOM pools, yet both landscape types place similar cumulative pressure on ecosystems.

In lakes, I found that the combination of nutrients and DOM leads to stronger microbial activity than either input alone. Nutrient enrichment allows microbes to break down DOM more efficiently, but this also results in greater release of carbon dioxide. This demonstrates a trade-off: nutrient-rich conditions may increase carbon uptake into microbial biomass, but they also accelerate greenhouse gas production. I also tested how lakes respond to repeated pulses of DOM. Systems with historically low DOM showed difficulties adjusting to extreme inputs of DOM, while brown lakes already rich in organic matter showed lower accumulation of DOM, suggesting that background conditions shape how aquatic systems handle disturbances.

Finally, I examined how constructed wetlands can be designed to better remove DOM before it reaches downstream lakes and coastal waters. Shallow zones promote photodegradation by sunlight, while deeper zones favor microbial degradation. Multi-depth designs that combine these zones can therefore process DOM under a wider range of seasonal conditions. However, wetlands are not a silver bullet. They should be viewed as one tool in an integrated catchment management strategy, alongside measures such as reducing nutrient inputs, restoring riparian vegetation, and adjusting land-use practices.

Overall, this thesis shows that the processing of organic carbon in freshwaters is controlled not only by the amount of DOM entering systems, but also by when it arrives, where it comes from, and how it interacts with nutrients. By understanding these dynamics, we can design more effective strategies to safeguard water quality, limit greenhouse gas emissions, and strengthen the resilience of aquatic ecosystems in a changing climate.

Populärvetenskaplig sammanfattning

Många av oss har nog lagt märke till att sjöar, vattendrag och kustvatten blir allt mörkare. Denna så kallade ”brunifiering” orsakas av ökande mängder löst organiskt material (DOM), som främst består av organiskt kol som lakas ut från jordar och vegetation. Brunt vatten är mer än bara en visuell förändring: det minskar siktdjupet, förändrar näringsvävar, driver på mikrobiell respiration och kan öka utsläppen av växthusgaser från inlandsvatten. Samtidigt utsätts många vattenmiljöer också för näringsberikning från jordbruk, skogsbruk och andra mänskliga aktiviteter. För att kunna förutse framtida vattenkvalitet och utveckla sätt att skydda akvatiska ekosystem är det avgörande att förstå hur kol och näringsämnen samverkar.

I min forskning har jag studerat hur mängden och kvaliteten på DOM varierar med årstider och mellan landskapstyper, samt hur mikrober reagerar när DOM och näringsämnen tillförs tillsammans. Genom att kombinera fältstudier i vattendrag och sjöar med kontrollerade mesokosmexperiment kunde jag undersöka både naturlig variation och specifika experimentella manipulationer. Resultaten visar att DOM som exporteras under vår- och höstregn är särskilt biotillgänglig, vilket innebär att det snabbt konsumeras av mikrober och leder till konsumtion av syre. Jordbruksdominerade avrinningsområden bidrar med mer biotillgängligt DOM, medan skogstäckta avrinningsområden exporterar större mängd men mer svårnedbrutet DOM. Transport från båda landskapstyperna kan därmed leda till lägre syrekoncentration i ekosystemen.

I sjöar fann jag att kombinationen av näringsämnen och DOM leder till starkare mikrobiell aktivitet än vartdera tillskottet ensamt. Näringsberikning gör det möjligt för mikrober att bryta ner DOM mer effektivt, men detta resulterar också i ett större utsläpp av koldioxid. Detta visar på en avvägning: näringsrika förhållanden kan öka kolupptaget i mikrobiell biomassa, men de påskyndar samtidigt produktionen av växthusgaser. Jag testade också hur sjöar reagerar på upprepade pulser av DOM. System med historiskt låga DOM-nivåer hade svårare att anpassa sig till och bryta ner extrema pulser, medan bruna sjöar som redan är rika på organiskt material visade lägre ackumulering av DOM. Detta tyder på att bakgrundsförhållanden påverkar hur vattenmiljöer hanterar störningar.

Slutligen undersökte jag hur konstruerade våtmarker kan utformas för att bättre avskilja DOM innan det når sjöar och kustvatten. Grunda zoner främjar nedbrytning av solljus, medan djupare zoner gynnar mikrobiell nedbrytning. Konstruktioner som kombinerar zoner med olika djup kan därför bearbeta DOM under större delen av året. Våtmarker är dock ingen universallösning. De bör ses som ett verktyg i förvaltning som tillsammans med åtgärder såsom att minska näringstillförseln, återställa strandnära vegetation och anpassa markanvändningen kan leda till bättre vattenkvalité.

Sammanfattningsvis visar denna avhandling att omsättningen av organiskt kol i sötvatten inte bara styrs av mängden DOM som tillförs systemen, utan också av när det sker, varifrån det kommer och hur det samverkar med näringsämnen. Genom att förstå dessa dynamiker kan vi utforma mer effektiva strategier för att bevara vattenkvalitet, begränsa utsläpp av växthusgaser och stärka resiliensen hos akvatiska ekosystem i ett föränderligt klimat.

Introduction

Aquatic ecosystems play a central role in the global carbon cycle, acting as both transporters and transformers of organic carbon. Dissolved organic matter (DOM) is a chemically complex mixture of organic molecules derived from terrestrial and aquatic sources (Kellerman et al., 2020). DOM regulates biogeochemical processes such as nutrient cycling, microbial metabolism, and greenhouse gas fluxes, making it a crucial component of freshwater ecosystem functioning (Cole et al., 2007; Kritzberg et al., 2020; Tranvik et al., 2009). DOM contains humic substances, proteins, amino acids, carbohydrates, and lipids, serving as an essential energy source for microbial communities that drive carbon transformations in lakes, rivers, and coastal areas (Berggren et al., 2018; Jansson et al., 2000). Understanding DOM dynamics is particularly critical in boreal and temperate freshwater systems, where shifts in land use, climate change, and nutrient loading are altering its composition, bioavailability, and ecosystem-level impacts. In recent decades, two major environmental stressors have emerged as dominant forces affecting DOM cycling in northern European freshwaters: brownification and eutrophication (de Wit et al., 2016; Monteith et al., 2007). Because these lakes and rivers ultimately connect to coastal seas, changes in DOM quantity and quality can propagate downstream, influencing oxygen dynamics, microbial processing, and carbon cycling in marine ecosystems such as the Baltic Sea (Asmala et al., 2013; Soares et al., 2019).

The Baltic Sea: A System Under Pressure

The Baltic Sea is one of the world's most heavily impacted coastal marine ecosystems, suffering from chronic hypoxia, eutrophication, and increasing terrestrial organic matter inputs (Hepach et al., 2024). Its limited water exchange with the North Sea, combined with a large watershed spanning multiple countries, makes the Baltic particularly sensitive to riverine inputs of bioavailable DOM. High loads of terrestrially derived organic matter and nutrients from rivers contribute to oxygen depletion, altered microbial activity, and shifts in primary production, exacerbating coastal hypoxia and bottom-water anoxia (Asmala et al., 2013; Berggren et al., 2018). DOM bioavailability is a critical factor in these processes: labile (easily degradable) DOM fractions drive microbial respiration and carbon turnover, while recalcitrant fractions contribute to long-term carbon storage and light attenuation in the water column (Fan et al., 2024; Malik & Gleixner, 2013; Osburn & Bianchi, 2016). While hypoxia in the Baltic Sea is commonly associated with anthropogenic nutrient enrichment, recent work has also emphasized the role of enhanced organic matter (OM) transport from land in fueling microbial respiration and expanding oxygen-depleted zones (Conley et al., 2011). Historically, eutrophication was considered the dominant driver of hypoxia, but evidence now suggests that rising terrestrial OM inputs, especially in coastal zones, are an important and often underestimated contributor. Although natural hypoxia has occurred in the Baltic's deep basins for millennia, its frequency, intensity, and spatial extent have increased sharply in recent decades due to the combined effects of nutrient enrichment, DOM loading, and climate-driven stratification (Conley et al., 2011).

The Rising Pressures of Brownification and Eutrophication

Brownification, characterized by increasing inputs of terrestrial DOM that darken water bodies, has intensified due to multiple factors including land-use changes, climate-driven increases in precipitation, and recovery from historical acid deposition (de Wit et al., 2016; Kritzberg & Ekström, 2012; Monteith et al., 2007). In marine environments, this process is often referred to as coastal darkening, reflecting similar mechanisms of increased terrestrial DOM transport and associated light attenuation (Andersson et al., 2015; Asmala et al., 2013). This influx of organic matter, rich in recalcitrant humic substances, reduces light penetration, alters microbial community structure, and impacts primary production, leading to shifts in aquatic food webs and metabolic balance (Kellerman et al., 2014; Kothawala et al., 2014). Eutrophication, driven by excessive nutrient loading from agricultural and urban runoff, has simultaneously caused profound ecological imbalances. By increasing autochthonous (within-lake) DOM production, eutrophication promotes harmful algal blooms, oxygen depletion, and changes in microbial processing efficiency (Brailsford et al., 2019; Mattsson et al., 2009). Despite short-term variability across systems, long-term analyses show that shallow lakes exhibit consistent stoichiometric relationships between nutrient ratios and phytoplankton biomass, reinforcing the predictability of eutrophication responses (Graeber et al., 2024). These dual stressors affect both lake and coastal ecosystems, where altered DOM dynamics contribute to changes in oxygen availability, biodiversity, and greenhouse gas production (Asmala et al., 2013; Meier et al., 2012; Solomon et al., 2015). Together, brownification and eutrophication generate complex and sometimes unpredictable consequences for carbon cycling, influencing greenhouse gas emissions, carbon sequestration, and microbial respiration (Bastviken, Cole, et al., 2004; Berggren et al., 2012). It is therefore essential to examine not only their individual effects but also their interactions, as these combined pressures shape ecosystem function in nonlinear ways

The Role of Constructed Wetlands in Mitigating DOM Transport

Constructed wetlands (CWs) are human-made systems designed to mimic natural wetlands for the purpose of treating water, particularly in agricultural or urban landscapes (Mitsch et al., 2015). They are distinct from created wetlands, which are often designed for ecological restoration or habitat replacement. CWs are increasingly used as a management tool to reduce the transport of DOM and nutrients to downstream aquatic ecosystems. These engineered ecosystems facilitate the removal of DOM, nitrogen, and phosphorus through processes such as photodegradation, microbial degradation, plant uptake, and sedimentation (Mitsch et al., 2015; Overton et al., 2023; Sardana et al., 2019; Vymazal, 2007; Zhao et al., 2024). By filtering and transforming organic matter before it enters larger water bodies, CWs help improve water quality and mitigate the impacts of eutrophication and brownification. However, optimizing wetland design, such as water depth and residence time, to effectively retain or transform bioavailable DOM fractions remains an open research challenge. Understanding how factors like water depth and seasonal conditions influence DOM processing in wetlands is crucial for improving their performance as DOM and nutrient sinks.

Knowledge Gaps and Research Needs

Despite substantial progress in understanding DOM dynamics, several key uncertainties remain. First, while it is well established that DOM export varies strongly with hydrology and seasonality in boreal catchments (Ågren et al., 2008; Ågren et al., 2007), the ecosystem-scale consequences of these pulses for microbial metabolism remain poorly constrained. Microbial growth efficiency and respiration have been shown to depend on DOM quality and nutrient context (Berggren et al., 2007; Guillemette & del Giorgio, 2011), yet the links between seasonal DOM inputs and microbial carbon use efficiency at the ecosystem scale are still not well resolved.

Second, brownification and eutrophication are typically studied in isolation, even though they increasingly co-occur in many northern and temperate lakes. Rising terrestrial DOM inputs alter light penetration and microbial substrate availability (Klante et al., 2021; Kritzberg et al., 2020), while nutrient enrichment stimulates autochthonous DOM production and respiration (Brailsford et al., 2019). How these stressors interact to regulate microbial carbon cycling, including shifts in respiration versus biomass incorporation, remains an important open question (Fonvielle et al., 2016).

Third, although constructed wetlands are widely applied to reduce nutrient export (Braskerud et al., 2005; Kadlec & Wallace, 2008), their role in transforming and retaining DOM has received far less attention. Evidence suggests that wetland design features such as depth and residence time strongly regulate the balance between photochemical and microbial DOM processing (Borgström et al., 2024; Catalán et al., 2016; Li et al., 2008), but systematic evaluations across seasonal conditions are scarce. Understanding these controls is crucial if wetlands are to serve as effective tools for reducing terrestrial DOM transport and mitigating both brownification and downstream oxygen depletion.

Research Aims and Questions

Given the ecological importance of DOM in freshwater and coastal systems, this thesis examines how natural variability and management interventions shape DOM dynamics. Specifically, it investigates seasonal fluctuations in DOM export, microbial responses to changes in DOM quantity and quality, and the capacity of constructed wetlands to mitigate downstream DOM transport and transformation.

Specifically, this work addresses the following research questions:

1. How do seasonal and event-driven changes in DOM inputs influence microbial processing and carbon bioavailability?

This question is addressed by combining results from **Papers I, II, and III**, which examine DOM inputs during different seasons (winter, spring, summer, autumn), under both continuous and pulse loading regimes, and across contrasting lake types. These studies quantify how DOM composition and microbial responses shift in relation to catchment type, seasonality, and pulse characteristics, shedding light on the mechanisms by which climate-driven changes may alter carbon turnover and respiration in aquatic systems.

2. What are the interactive effects of brownification and eutrophication on microbial carbon cycling in freshwater ecosystems?

In **Paper II**, experimental manipulations with DOM extract (proxy for brownification) and nutrients (proxy for eutrophication) were conducted simultaneously, allowing this thesis to explore how nutrient enrichment influences microbial utilization of terrestrial DOM, including effects on bacterial production, respiration, and carbon use efficiency. These results help clarify how multiple stressors may amplify or mitigate each other's impacts on carbon fluxes in lakes.

3. How can constructed wetlands be designed to optimize DOM removal and reduce downstream brownification and associated risks of hypoxia across seasons?

Paper IV focuses on how wetland depth, water residence time, and seasonal conditions affect DOM degradation through microbial and photochemical pathways. This research contributes to understanding how nature-based solutions can be tailored to improve year-round removal of bioavailable and humic DOM from the landscape.

These three integrated research questions form the thematic basis of this thesis, which advances our understanding of DOM transformations in aquatic ecosystems under both natural variability and human influence.

Dissolved Organic Matter (DOM) Characteristics and Transformation Processes

DOM in aquatic systems is a chemically diverse mixture of organic compounds originating from both terrestrial and aquatic sources (Detweiler et al., 2025; Gad et al., 2025). It serves as a key intermediary in global carbon cycling, regulating microbial metabolism, nutrient availability, and greenhouse gas emissions (Carlson & Hansell, 2015; Kothawala et al., 2015). The composition and fate of DOM are shaped by various biological and environmental processes, which influence its bioavailability and degradation rates (Vaziourakis et al., 2025). Before exploring the dynamic processing of DOM in ecosystems, it is important to understand its sources and the transformation pathways it undergoes.

Sources and Composition of DOM

DOM can be classified by origin as allochthonous or autochthonous. Allochthonous DOM is transported from terrestrial environments into aquatic ecosystems via surface runoff, soil leaching, and groundwater discharge (Lapierre & Frenette, 2009; Tranvik et al., 2009). It is typically dominated by high-molecular-weight, aromatic compounds such as humic and fulvic acids (Berggren et al., 2018; Kritzberg et al., 2004). These compounds contribute to chromophoric DOM (CDOM, the light-absorbing component of DOM) and are relatively resistant to microbial degradation (Helms et al., 2008; Kothawala et al., 2014). This recalcitrant, humic-rich fraction strongly influences watercolor and can contribute to long-term carbon storage in lake sediments and ocean outflows (Tranvik et al., 2009).

In contrast, autochthonous DOM is produced within the aquatic ecosystem itself, primarily through phytoplankton and macrophyte exudation, algal cell lysis, and microbial byproducts (Bertilsson & Tranvik, 2000; Jansson et al., 2000). Autochthonous DOM tends to be more labile, consisting of low-molecular-weight compounds such as simple carbohydrates, amino acids, and peptides that readily fuel microbial metabolism (Berggren et al., 2012; Koehler et al., 2012). The balance between allochthonous and autochthonous DOM inputs varies seasonally and spatially, depending on factors like hydrology (e.g. rain events, groundwater flow), light availability for primary production, and nutrient concentrations (Guillemette & del Giorgio, 2011; Lapierre & Frenette, 2009). For instance, during spring floods, terrestrial inputs dominate DOM pools, whereas in mid-summer, in-lake primary production can increase the proportion of autochthonous DOM.

Understanding the mixture of DOM sources is important because it sets the stage for how DOM will be processed. Generally, terrestrial DOM (allochthonous) is more aromatic and less bioavailable, while aquatic DOM (autochthonous) is more protein-like and readily utilized by microbes. This inherent compositional difference influences which transformation processes (photochemical vs. biological) are likely to be most effective.

Transformation Pathways of DOM

Once in the aquatic environment, DOM is transformed through two main categories of processes that determine its ultimate fate: mineralized to CO_2 or CH_4, incorporated into biomass, or downstream export (Bauer & Bianchi, 2011; Burd et al., 2016; Fischer, 2003). These processes do not act in isolation; rather, they often interact in sequence or in tandem, creating feedback loops in DOM cycling. Broadly, the two categories of processes are:

Abiotic transformations: Primarily photochemical degradation and oxidative reactions.

Biotic transformations: Microbial uptake and metabolism, including both respiration and biomass production.

Both pathways can significantly alter DOM concentration and composition on timescales ranging from hours (for photoreactions) to weeks (for microbial processing). Physical processes such as flocculation and sedimentation also affect the transport and removal of DOM, but they do not transform its chemical composition and are therefore treated separately from transformation pathways.

Abiotic Processes

One dominant abiotic transformation is photodegradation, in which exposure to solar ultraviolet (UV) and visible light chemically alters DOM. Sunlight can break complex, high-molecular-weight DOM molecules into smaller, more bioavailable compounds for microbial uptake (Cory et al., 2014; Moran & Zepp, 1997). Photodegradation can also directly mineralize DOM, converting dissolved organic carbon into inorganic carbon (CO_2) without biological involvement (Bertilsson & Tranvik, 2000; Koehler et al., 2014). This process is particularly important in sunlit surface waters of lakes and wetlands. In shallow systems with high UV penetration, photochemical reactions can substantially lower DOM concentrations and alter DOM quality over the course of a summer season (Cory et al., 2014; Koehler et al., 2014). For example, in shallow wetlands, photodegradation has been observed to significantly reduce aromatic DOM components during sunny periods (Cory & Kling, 2018; Waiser & Robarts, 2004).

Another key abiotic process is chemical oxidation by reactive species such as hydroxyl radicals ($\cdot OH$) and hydrogen peroxide (H_2O_2). These oxidants can be produced in situ (often as byproducts of photochemical reactions) and can further break down DOM molecules (Kieber et al., 2003; Vähätalo & Wetzel, 2004).

Oxidative fragmentation of DOM can increase its bioavailability by producing smaller organic acids and aldehydes, or conversely, completely oxidize DOM to CO_2 (Kujawinski et al., 2004). While chemical oxidation is harder to directly observe in situ than photodegradation, it is an important route for DOM transformation, especially in environments with high iron or metal content that catalyze radical formation (Lueder et al., 2020). In addition to these direct chemical reactions, abiotic processes can also influence the organization of DOM. For example, interactions with metals such as iron and aluminum can promote colloid formation or flocculation, which alters DOM stability and light absorption properties (Andersson et al., 2025; von Wachenfeldt & Tranvik, 2008). Photochemical reactions may further destabilize or fragment colloids, linking abiotic drivers to changes in DOM persistence.

It is worth noting that abiotic processes often set the stage for biotic ones: photodegradation can yield labile photoproducts that microbes eagerly consume, while partial oxidation can remove chromophores, allowing light to penetrate deeper, or in some cases, generate colored byproducts (Kiki et al., 2024). Thus, the end of an abiotic process often marks the beginning of a biotic process in the DOM cycle.

Biotic Processes

Microbial activity is a major driver of DOM transformation. Heterotrophic bacteria (and other microbes like fungi and archaea) utilize DOM compounds as carbon and energy sources, through processes of assimilation (building biomass) and respiration (oxidizing organic carbon to CO_2 for energy) (Moran et al., 2022; Taube et al., 2018). Generally, labile DOM such as simple sugars, amino acids, and other protein-like components are rapidly consumed by bacteria, whereas highly aromatic humic substances require specialized enzymes and longer timeframes to degrade (Arnosti, 2011; Berggren et al., 2012). In some cases, however, the availability of labile DOM can stimulate microbial communities to also degrade more refractory, humic-rich compounds, a mechanism known as “priming” (Bianchi, 2011; Guenet et al., 2010). Beyond molecular composition, the physical organization of DOM can also constrain microbial access. In soils, persistence is often explained by mineral associations and aggregation (Lehmann & Kleber, 2015), while in aquatic systems, metal–DOM complexes and colloidal assembly can reduce bioavailability. Recent work has shown that while molecular DOM is readily consumed, colloidal fractions may persist for months, indicating that supramolecular structure can limit microbial degradation even in aqueous environments (Boye et al., 2025). This process highlights how changes in DOM quality can alter not only the direct utilization of labile substrates but also the longer-term breakdown of otherwise resistant organic matter.

The efficiency with which microbes convert DOM into biomass vs. respired CO_2 is described by the bacterial growth efficiency (BGE) (Fonte et al., 2013). DOM with balanced nutrients (e.g. appropriate carbon:nitrogen:phosphorus ratios) tends to support higher BGE, meaning more of that carbon ends up in microbial biomass (Berggren et al., 2007; Jansson et al., 2006). Conversely, DOM that is nutrient-poor or very rich in carbon relative to nutrients often leads to excess carbon being respired as CO_2 (Graeber et al., 2021; Neff et al., 2000). Experimental evidence supports this mechanism, showing that microbial nutrient assimilation is directly constrained by the ratio of bioavailable DOC to reactive nitrogen and phosphorus, consistent with the macronutrient-access hypothesis (Graeber et al., 2021). For example, in systems dominated by carbon-rich, nutrient-poor terrestrial DOM, bacteria may use much of that carbon for energy (CO_2 release) rather than growth, resulting in low growth efficiency. In contrast, algal-derived DOM (which can be more N and P rich) or DOM in a nutrient rich environment allows bacteria to incorporate a higher fraction of carbon into biomass (Jansson et al., 2006).

Seasonal conditions strongly influence microbial DOM processing. Warmer temperatures typically enhance metabolic rates, so bacterial production and respiration increase in summer. In temperate lakes, it is common to see an increase in bacterial activity in late spring and summer when both temperature and availability of labile DOM (from spring algal blooms or inputs) are high (Kritzberg et al., 2006; Pace et al., 2021). In winter, colder temperatures and sometimes ice cover slow microbial processes significantly, causing DOM to accumulate or be preserved longer (Kurek et al., 2022). Oxygen availability is also crucial: in stratified water bodies, microbial DOM degradation in bottom waters may be limited by low oxygen, shifting the process to slower anaerobic pathways (Bastviken, Persson, et al., 2004; Chen et al., 2022). Importantly, microbes can alter DOM composition as they feed. They preferentially consume certain compounds (e.g. sugars, organic acids), leaving behind more recalcitrant material (Koch et al., 2014; Lehmann et al., 2020). They also produce new DOM compounds in the form of metabolic byproducts and cell lysis products. This microbial reworking can reduce the aromaticity of DOM and increase the proportion of protein-like components over time, although these labile compounds are often rapidly consumed by microbes and may not persist. Nonetheless, transient increases in protein-like DOM can temporarily alter optical properties and enhance DOM susceptibility to further photodegradation (Antony et al., 2018; Goranov et al., 2022). Biotic and abiotic processes therefore form a continuum: what microbes leave behind may be further degraded by sunlight, and vice versa.

Factors Influencing DOM Transformations

The rate and extent of DOM transformation depend on both intrinsic properties of the DOM and extrinsic environmental factors. Intrinsic factors include molecular weight, aromaticity (often quantified by Specific UV Absorbance at 254 nm, $SUVA_{254}$), and the presence of certain functional groups (e.g. phenolic hydroxyls) that influence DOM's reactivity to light or enzymes (Berggren et al., 2018; Kothawala et al., 2015). For example, DOM with high aromatic content is more susceptible to photobleaching but less readily metabolized by microbes lacking the necessary enzymes. Conversely, DOM rich in amino acids or simple sugars is highly bioavailable but may not absorb light significantly (Benner & Kaiser, 2011; Sulzberger & Durisch-Kaiser, 2009).

Extrinsic factors include temperature, light exposure (UV intensity and duration), oxygen levels, nutrient concentrations, and water residence time (WRT). Temperature and nutrients generally enhance microbial degradation rates (Berggren & del Giorgio, 2015). UV exposure drives photodegradation as discussed. Oxygen is needed for aerobic microbial respiration and certain photochemical reactions. WRT is particularly important in lentic systems and wetlands: longer residence times allow more complete processing of DOM via both photochemical and microbial pathways, whereas short residence can export DOM before it is extensively altered (Catalán et al., 2016). Studies by Weyhenmeyer et al. further indicate that both the degradation of dissolved organic carbon and reductions in watercolor (via preferential removal of chromophoric DOM) are closely linked to WRT, with longer durations favoring greater in-system transformation (Weyhenmeyer et al., 2012).

For instance, consider a shallow lake or wetland with a long residence time in summer: ample sunlight and slow flushing lead to significant photodegradation and subsequent microbial consumption of DOM, meaning by the time water leaves the system, its DOM load is much reduced. In contrast, during a spring flood in a river with very short residence time, large amounts of DOM can be washed downstream with minimal in-system processing, delivering a pulse of aromatic, land-derived DOM to downstream waters (Raymond & Spencer, 2015). Hydrology thus modulates the relative importance of in-system processing vs. export.

Overall, understanding the source and compositional attributes of DOM, and the conditions of the environment, is essential for predicting DOM's fate. This background sets the foundation for the following sections, which explore how seasonal variability, landscape context, and human-induced changes influence DOM dynamics, and how we might mitigate undesirable DOM export.

Methods

Analytical Techniques and Study Sites

Understanding DOM dynamics and transformations requires robust analytical tools to characterize its composition, reactivity, and biological lability. In this thesis, a combination of optical measurements and biogeochemical assays was used to track both the chemical quality of DOM and its microbial utilization. This section is divided into two parts: DOM characterization and microbial processing.

DOM Characterization Techniques

Spectroscopy has become a standard technique for characterizing DOM due to its sensitivity and affordability (Hansen et al., 2016). DOM can be divided into optically active fractions, chromophoric DOM (CDOM), which absorbs light, and fluorescent DOM (FDOM), which emits fluorescence when excited by specific wavelengths. CDOM is typically quantified via UV-Vis absorbance (e.g., a254, a420), whereas FDOM is measured using excitation-emission matrices (EEMs) and interpreted with PARAFAC (Coble, 1996; Stedmon & Bro, 2008).

Absorbance-Based Metrics (CDOM)

Chromophoric dissolved organic matter (CDOM) refers to the fraction of DOM that absorbs light, particularly in the ultraviolet and visible ranges. UV-Vis spectrophotometry was used to assess CDOM quality. Absorbance at 254 nm (A254) was measured to calculate the Specific UV Absorbance at 254 nm (SUVA254) by normalizing to DOC concentration (Weishaar et al., 2003). SUVA is a widely used proxy for DOM aromaticity, with higher values indicating more humic, terrestrially derived, and potentially recalcitrant DOM.

Additionally, absorbance at 420 nm (a420) was recorded to estimate watercolor by multiplying a420 by 500 (Pennanen, 1986). These absorbance metrics provided a coarse but rapid indication of DOM source and lability.

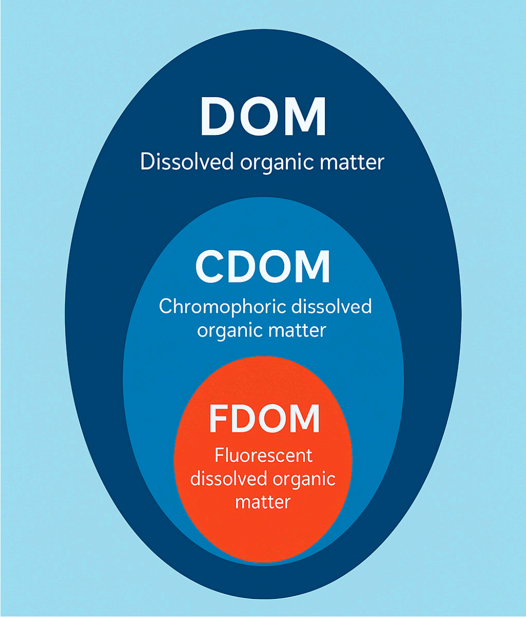

Figure 1. Conceptual illustration of the relationship between dissolved organic matter (DOM), chromophoric DOM (CDOM), and fluorescent DOM (FDOM).

Fluorescence Spectroscopy (FDOM) and PARAFAC

Fluorescent DOM (FDOM) was analyzed via excitation-emission matrix (EEM) fluorescence spectroscopy. This 3D data captures fluorescence intensity across a grid of excitation and emission wavelengths. Peaks corresponding to known fluorophores were monitored (Figure 2):

- Peak A (Ex 260 nm / Em 400–460 nm): humic-like, terrestrial origin
- Peak C (Ex 320–360 nm / Em 420–460 nm): humic-like, terrestrial origin
- Peak M (Ex: ~290–310 nm / Em: ~370–410 nm): Microbial humic-like, often associated with reworked or aquatic DOM
- Peak B (Ex 275 nm / Em 305 nm): protein-like, tyrosine
- Peak T (Ex 275 nm / Em 340 nm): protein-like, tryptophan (Coble, 1996)

To decompose these EEMs into their component signals, we applied Parallel Factor Analysis (PARAFAC), a multivariate statistical approach well-suited for complex DOM samples (Murphy et al., 2013; Stedmon et al., 2003). This enabled us to track specific fluorescent components through time and treatments, helping identify photochemical or microbial transformation processes.

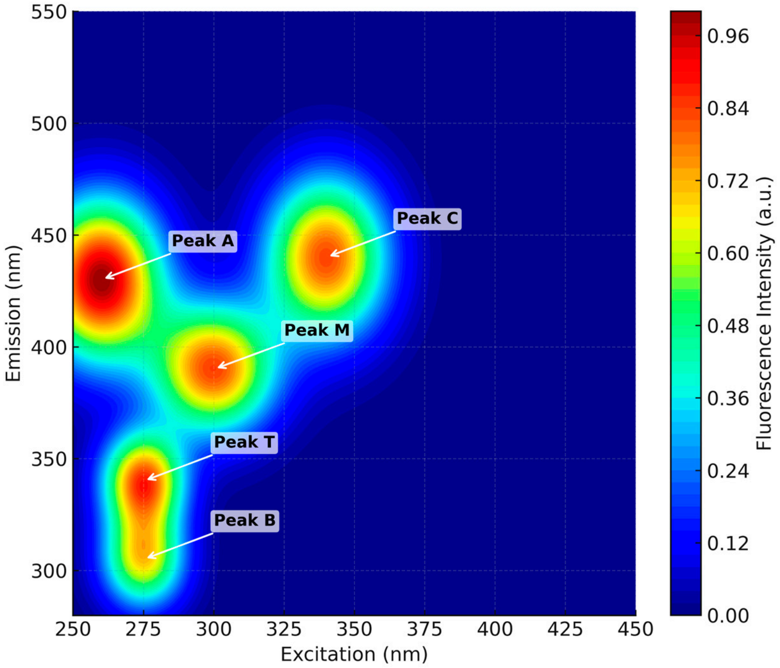

Figure 2. Representative excitation–emission matrix (EEM) illustrating characteristic fluorescence peaks of dissolved organic matter (DOM) (Coble, 1996). Peaks A and C represent humic-like, terrestrially derived DOM; Peak M indicates microbial humic-like DOM; Peaks B and T correspond to protein-like fluorescence (tyrosine- and tryptophan-like, respectively).

Spectral Slopes

Spectral slope parameters were calculated from UV–Vis absorbance spectra to assess DOM molecular weight distribution and degradation processes. The slope ratio (SR = S275–295 / S350–400) increases with decreasing molecular weight and is widely used as a proxy for photochemical breakdown (Helms et al., 2008). Photodegradation typically produces higher SR values by fragmenting large, aromatic molecules into smaller, less colored compounds. In contrast, microbial degradation often results in lower SR values, as microbes preferentially consume low-molecular-weight, labile fractions rather than extensively altering aromatic structures (Helms et al., 2008; Mostovaya et al., 2017).

Spectral slopes therefore provide a useful diagnostic tool to distinguish the relative importance of UV-driven versus biologically driven DOM transformations. In **Paper III**, seasonal differences in SR helped identify when photochemical processes dominated DOM alteration, whereas in **Paper IV**, slope changes between shallow and deep wetland mesocosms highlighted how light availability shaped DOM removal pathways. Together, these applications demonstrate how spectral slope analysis links molecular-scale changes to ecosystem-level DOM dynamics. Figure 3 conceptually illustrates this trajectory, showing how photodegradation increases SR, microbial degradation decreases SR, and combined processes often yield intermediate or variable values.

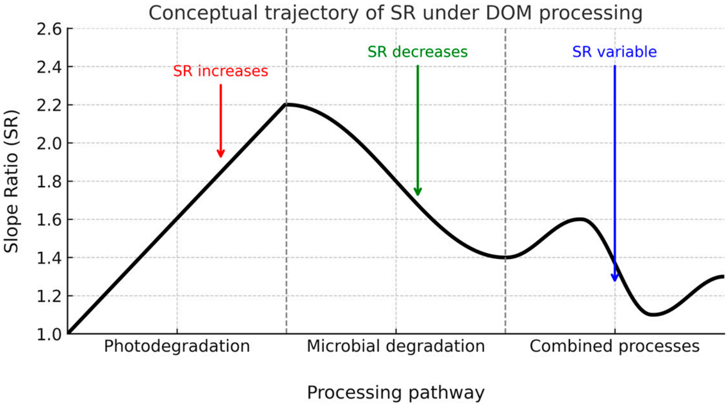

Figure 3. Conceptual trajectory of the slope ratio (SR) under different DOM processing pathways. During photodegradation, SR increases as sunlight fragments aromatic, high-molecular-weight compounds into smaller molecules with steeper short-wavelength absorbance slopes. In contrast, microbial activity leads to declining SR because microbes preferentially consume labile, low-molecular-weight fractions, leaving more aromatic material behind. When photochemical and microbial processes act together, SR typically fluctuates, reflecting the balance between opposing mechanisms.

Microbial Process Measurements

To assess DOM lability and microbial utilization, we used standard techniques to measure bacterial production, respiration, and growth efficiency, offering a direct view of carbon processing.

Bacterial Production (BP)

Bacterial production (BP) was measured via leucine incorporation, a method that tracks the uptake of radiolabeled leucine, an amino acid used in protein synthesis (Bååth et al., 2001; Smith & Azam, 1992). When offered in saturating concentrations, bacteria incorporate this labeled precursor into newly formed biomass, allowing estimation of new bacterial carbon production rates.

This method assumes known values for cellular protein content and leucine composition to convert uptake into carbon units. BP reflects the capacity of microbes to convert DOM into biomass.

Bacterial Respiration (BR)

Respiration was quantified using biological oxygen demand (BOD) incubations over 5 days. Oxygen consumption in sealed bottles was measured via two complementary methods:

- Winkler titration: A classical wet-chemistry method involving $MnCl_2$ and an alkaline iodide solution (NaOH + NaI), followed by acidification and titration with $Na_2S_2O_3$ (Murray et al., 1968; Winkler, 1888). This method provides precise endpoint measurements of O_2 depletion but does not capture temporal dynamics.
- Oxy-10 PreSens® sensors: Fiber optic probes recorded oxygen concentration every 30 minutes, generating continuous high-resolution respiration curves. These data reveal both initial rates and nonlinear dynamics of microbial oxygen demand often missed in endpoint-based methods.

Rates of O_2 consumption were converted into CO_2 equivalents assuming a respiratory quotient of 1 (Dodds & Whiles, 2010; Soares et al., 2019). This conversion allows direct comparison between respiration and bacterial production. In the context of this thesis, BR serves as a key indicator of DOM lability: higher respiration rates reflect rapid microbial turnover of labile DOM fractions, while lower rates suggest dominance of more recalcitrant substrates.

Bacterial Growth Efficiency (BGE)

Bacterial growth efficiency was calculated as: BGE = BP / (BP + BR) (Giorgio & Cole, 1998). This metric expresses how efficiently bacteria convert DOM into biomass rather than respiring it. Across natural aquatic systems, reported BGE values span a wide range from as little as ~1% in oligotrophic waters to upwards of 50–60% in nutrient-rich systems with most freshwater values typically falling within 5–40% (Apple & del Giorgio, 2007; Berggren et al., 2007; del Giorgio & Cole, 1998; Fonte et al., 2013). These differences reflect variation in DOM quality, nutrient availability, and environmental context.

By combining these techniques: fluorescence EEMs, absorbance, and microbial assays, we assembled a robust picture of DOM transformations. Each method has its strengths: optical measures are immediate and sensitive to composition changes, while biodegradation tests reveal actual ecological impact (how much DOM microbes can consume). Using them together, observed changes in DOM quality (e.g., a drop in humic fluorescence and SUVA, a rise in SR) were linked to expected functional outcomes in microbial carbon processing (e.g., increased microbial uptake, which we then confirmed via respiration or bacterial production tests). This integration also provided context for interpreting dominant processes: for instance, whether DOM loss was primarily linked to UV-driven photodegradation (inferred from optical shifts) or to microbial metabolism (supported by respiration and production rates).

Study Facilities and Experimental Platforms

The field study in **Paper I** was conducted in nine river mouths draining into the Baltic Sea: Helgeå, Lyckebyån, Alsterån, Emån, Ljungbyån, Kävlingeån, Mörrumsån, Skivarpsån, and Råån (Figure 4). These rivers represent catchments dominated by either forested or agricultural land use, providing a gradient of DOM sources and qualities. Sampling campaigns were performed seasonally and under varying hydrologic conditions, with water collected at river mouths for analyses of DOC, DOM absorbance (e.g., SUVA), and microbial bioassays (BR and BP).

Figure 4. Sampling location at Alsterån

Figure 5. Visualization of SITES AquaNet platform.

The experiments in **Papers II** and **III** were conducted at the SITES AquaNet platform, part of Sweden's national research infrastructure for ecosystem science (Figure 5). AquaNet consists of five lake facilities (Asa, Bolmen, Erken, Skogaryd, Svartberget) spanning a 760 km latitudinal gradient, enabling manipulations under diverse climatic and trophic conditions. At Lakes Bolmen and Erken, 700 L floating mesocosms (1.5 m deep, 0.8 m diameter) were mounted within modular Jetfloat platforms. The mesocosms can be equipped with autonomous sensors to log DO, temperature, PAR, chlorophyll-a, phycocyanin, and turbidity at high frequency. Integrated water column samples are collected with a Ruttner sampler for analyses of DOC, nutrients, DOM absorbance and fluorescence, microbial abundance, and plankton. Data loggers connected to central servers allow for real-time remote monitoring, ensuring comparability and standardization across sites.

The experiment in **Paper IV** was conducted at the constructed wetland facility outside Halmstad, Sweden (Figure 6). The facility consists of 18 uniform constructed wetlands (10 × 4 m) where variables such as water depth (~0.3–0.6 m), vegetation, and inflow can be precisely controlled. Water is supplied through distribution wells that permit dosing of added substances, while outlet structures allow adjustments of water residence time. The long-term development of this facility has provided a unique resource for testing the effects of wetland design on hydrology, nutrient cycling, and organic matter processing under field-realistic conditions.

Figure 6. Wetland Facility outside of Halmstad, Sweden

Results and Discussion

Four studies were conducted across different spatial and temporal contexts, to address the overarching questions of this thesis: (1) How do seasonal and event-driven changes in DOM inputs influence microbial processing and carbon bioavailability? (2) What are the interactive effects of brownification and eutrophication on microbial carbon cycling in freshwater ecosystems? (3) How can constructed wetlands be designed to optimize DOM removal and reduce downstream brownification and associated risks of hypoxia across seasons? The connection between each paper's focus, approach, and key findings is summarized in Table 1.

Paper I showed that DOM bioavailability varies seasonally and across catchments with contrasting land use. Based on repeated field sampling of river mouths draining forested and agricultural catchments into the Baltic Sea, we conducted standardized BR and BP assays to evaluate DOM lability, combined with SUVA to assess aromaticity. These parallel approaches allowed us to compare both chemical and microbial perspectives of DOM quality. DOM from agricultural streams was generally less aromatic and had a higher bioavailable fraction than DOM from forested catchments, which was more refractory. However, microbial oxygen demand responses were not always consistently different between land uses, and DOM utilization peaked during spring and autumn runoff in both systems. This suggests that hydrologic timing may play a stronger role than land cover alone, emphasizing the need for seasonally targeted management (Table 1).

Paper II focused on the interaction of brownification and eutrophication, using a mesocosm experiment at Lake Bolmen to isolate their individual and combined effects on DOM processing. We established replicated mesocosms with factorial additions of DOM extract and inorganic nutrients and monitored microbial responses over several days. BR, BP, and BGE were measured alongside optical properties to capture both functional and compositional changes. Measurements targeted the immediate microbial metabolic responses to a pulse of DOM and/or nutrients, with brownification increasing respiration and nutrient additions enhancing bacterial production. When combined, the two stressors increased microbial growth efficiency, showing non-additive, synergistic effects on microbial DOM uptake (Table 1).

Paper III investigated how DOM loading patterns influence microbial response by comparing episodic vs. continuous additions in mesocosms placed in two lakes, Lake Bolmen (humic, brown-water) and Lake Erken (clear-water), using a 36-day design utilizing SITES AquaNet infrastructure. Replicated mesocosms received either pulsed or continuous DOM additions, and BOD, fluorescence indices (FDOM) and SR were measured throughout to assess microbial metabolism and DOM quality changes over time. Pulsed DOM additions led to stronger microbial responses in the clear lake, while the humic lake exhibited a dampened response. This indicates that background DOM conditions mediate ecosystem sensitivity to loading dynamics (Table 1).

Paper IV explored seasonal DOM processing in shallow vs. deep constructed wetlands. Field-scale constructed wetlands (~0.3 m vs. ~0.6 m depth) were manipulated in summer and autumn, with DOM extract additions. The facility is located outside of Halmstad, Sweden. Replicated mesocosms were monitored for TOC, watercolor, DOM fluorescence (EEMs, PARAFAC components), SR, BR, BP, and BGE to track both compositional and microbial responses over time. During summer, shallow wetlands promoted rapid photodegradation of aromatic DOM, whereas deeper wetlands supported sustained microbial consumption. In autumn, microbial activity dominated in both wetland types. These findings suggest that combining wetland designs could maximize DOM removal across seasons, and that depth-driven light and microbial dynamics are critical to optimizing engineered solutions (Table 1).

Together, these studies reveal that DOM fate in aquatic systems is shaped by a combination of external drivers (e.g., hydrology, land use) and internal processing dynamics (e.g., light exposure, microbial metabolism). Effective management must integrate source-area controls with seasonally aware, in-system transformation processes.

Table 1. Overview of the four papers in the thesis, their guiding research questions, methodologies, key findings, and implications. Each study contributes to an integrated understanding of DOM dynamics, from source and seasonality (Paper I) to combined human impact factors (Paper II), to the influence of event-driven variability and system context (Paper III), and finally to mitigation strategies via engineered ecosystems (Paper IV)

Paper	Research question	Methodology	Key findings	Implications
I. Seasonal & land-use effects on DOM bioavailability	When and under what catchment conditions is exported DOM most bioavailable to downstream aquatic systems?	Year-long monitoring of forested vs. agricultural catchments; five time-points measuring DOM concentration, composition, and biodegradability.	Microbial DOM use peaked in spring and autumn runoff; land-use differences were minor compared to event timing.	Management should target high-flow and storm events rather than land use alone.
II. Brownification & eutrophication effects on microbial carbon utilization	What are the combined effects of brownification and eutrophication on microbial carbon utilization in lakes?	Mesocosm experiment in a brown-water lake with factorial DOM (peat) and nutrient (N & P) additions; measured BP, BR, BGE, and DOM optics.	Brownification increased respiration; nutrients stimulated production; combined treatments enhanced carbon use efficiency and DOM loss.	Nutrient controls may mitigate brownification, but combined inputs can accelerate turnover and greenhouse gas release.
III. Episodic vs. Continuous DOM loading in lakes with contrasting background conditions	How do episodic DOM loading events influence DOM bioavailability and microbial processing in lakes with differing water chemistry.	Mesocosms in humic vs. clear-water lakes; simulated pulsed vs. continuous DOM inputs with nutrients; monitored DOM optics and microbial responses.	Pulses caused stronger microbial responses in the clear-water lake, especially in spring; extreme pulses increased DOM loss and CO_2 release.	Lake type and season strongly mediate DOM responses to pulses, critical for predicting climate-driven changes.
IV. Optimizing constructed wetlands for DOM removal	How can constructed wetlands be optimized to maximize DOM removal and reduce downstream brownification and hypoxia across seasons?	Field test of shallow (~0.3 m) vs. deep (~0.6 m) wetlands in summer/autumn; DOM additions with DOM optics and microbial activity measured over 1–2 weeks.	Shallow wetlands favored summer photodegradation but re-released humic DOM; deep wetlands supported sustained microbial degradation, especially in autumn.	Hybrid designs with shallow + deep zones and seasonal adjustments can improve DOM removal and reduce brownification/ hypoxia.

Catchment Controls on DOM Quality and Bioavailability

Catchment land cover exerts a strong influence on the quality and lability of DOM entering aquatic systems. Forested catchments generally export DOM dominated by aromatic humic substances derived from soil organic matter, peat, and litter inputs. Humic substances are often high in carbon but chemically complex, reflected in high SUVA values and a greater proportion of refractory DOM (Mattsson et al., 2005; Pisani et al., 2020; Wilson & Xenopoulos, 2009). By contrast, agricultural catchments export DOM that is less aromatic and more nutrient-rich, including protein-like and fertilizer-derived compounds (Mattsson et al., 2009). At the same time, long-term monitoring has shown that point- and diffuse-source nutrient reductions often occur asynchronously, lowering nitrogen and phosphorus concentrations at different rates and thereby shifting riverine N:P ratios with important implications for DOM and nutrient interactions (Westphal et al., 2020).

Our results in **Paper I** confirmed these land cover contrasts. Rivers draining agricultural areas had consistently lower SUVA values and higher proportions of bioavailable DOM compared to forested catchments (Figure 7). Yet, at most time points, DOM bioavailability measured as BOD did not differ significantly between rivers draining forested and agricultural catchments. When differences did occur, agricultural systems tended to exhibit higher BOD, reflecting the greater proportion of labile DOM. However, forested catchments generally transported larger total DOM masses, both because of higher discharge and because of greater terrestrial organic matter inputs. Seasonal variability was also pronounced. Both forested and agricultural rivers exhibited peaks in DOM lability during spring and autumn, reflecting high runoff and nutrient mobilization. These temporal patterns emphasize that hydrology and timing interact with land cover in controlling DOM quality, as further illustrated in Figure 7. This highlights an important nuance: although agricultural DOM is chemically more labile, the combined hydrological and terrestrial inputs from forested systems mean they can dominate DOM export at the landscape scale (**Paper I**). **Paper I** also showed a seasonal contrast in aromaticity, with late-winter base flow samples exhibiting lower aromatic signatures than spring-runoff pulses; this observation is consistent with, but does not itself demonstrate, greater photolysis susceptibility when spring irradiance increases.

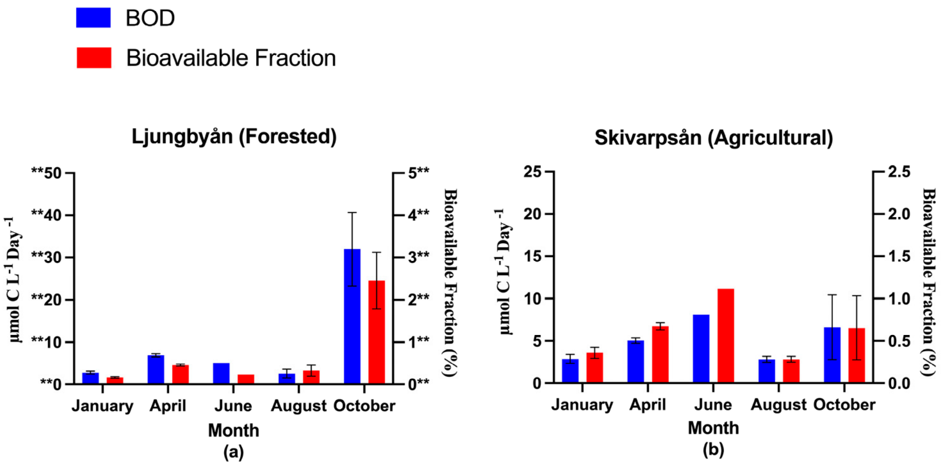

Figure 7. Seasonal variation in oxygen demand (BOD, blue) and the relative bioavailable fraction (red) in representative rivers draining forest dominated catchments (Ljungbyån) and agricultural dominated catchments (Skivarpsån). Values represent mean ± SD across replicate incubations. Agricultural catchments consistently exported a higher proportion of bioavailable DOM, while forested catchments exported larger total DOM pools with more refractory characteristics.

Spatial Gradients in DOM Processing

Beyond catchment differences, spatial gradients within and among lakes determine how DOM is processed. In **Paper III**, we compared a humic and a clear-water lake. Microbial communities in the humic lake responded quickly to added DOM, likely because they were already adapted to high terrestrial inputs. Photodegradation was relatively minor in this system, as light penetration was already low. In contrast, the clear-water lake exhibited slower microbial uptake of added DOM, while photodegradation played a greater role before microbial consumption. In the clear-water lake mesocosms, short-lived protein-like fluorescence peaks appeared but declined rapidly as microbes consumed the newly produced substrates (**Paper III**). These results demonstrate that background DOM conditions shape microbial responses to new inputs.

Within single lakes, spatial heterogeneity is also pronounced. Near inflows, DOM concentrations and allochthony are elevated, fueling respiration-dominated microbial activity (Calderó-Pascual et al., 2020; Hoke et al., 2020). In littoral zones, higher light and benthic surfaces favor photodegradation and biofilm-associated communities, while deep waters accumulate DOM that is degraded more slowly and sometimes under oxygen-depleted conditions (Calderó-Pascual et al., 2020; Prijac et al., 2022). Stratification further accentuates these differences, separating oxygen-rich, light-exposed surface waters from darker, oxygen-poor bottom layers (Liu et al., 2025).

Residence time is another critical spatial factor. As shown in prior work (Catalan et al., 2013), longer water residence times allow more extensive microbial processing, transforming DOM toward smaller and more oxidized molecules. In contrast, during high-flow events such as the spring and autumn runoff observed in **Paper I**, DOM was transported rapidly downstream with little opportunity for transformation (Figure 8). In these cases, it remained largely allochthonous from headwaters to outlet, underscoring how hydrology can override biological and photochemical processing.

Figure 8. High flow event at Mörrumsån in October 2020.

Seasonal Cycles of DOM Transformation

Seasonality adds a temporal dimension to the spatial and catchment effects described above, as both microbial and photochemical pathways vary with hydrology, light availability, and temperature. In **Paper I**, microbial oxygen demand peaked during spring and autumn runoff, when high terrestrial DOM loads entered rivers. These pulses contained both aromatic and labile fractions, stimulating respiration but often lowering BGE because much of the DOM was less bioavailable. **Paper I** indicated that DOM present during winter low-flow conditions had lower aromaticity than the more humic spring-runoff pulse. This is consistent with the idea that in-stream processing during winter may make DOM more susceptible to photodegradation when exposed to stronger spring sunlight, although this cannot be concluded with certainty.

In **Paper III**, we compared DOM processing between spring and summer in two lakes with contrasting baseline conditions. In Lake Bolmen (humic, high baseline CDOM), microbial activity remained relatively high in both seasons, with warmer summer conditions supporting elevated microbial respiration compared to spring. Lake Erken (clearer, lower baseline CDOM), the seasonal difference was more pronounced: spring DOM additions were rapidly assimilated, with protein-like peaks returning to control levels by Day 37, whereas summer additions led to more persistent fluorescence elevations despite stronger photochemical alteration. **Paper III** also showed that photochemical contributions differed between lakes: in Erken, higher light penetration allowed photodegradation to generate labile DOM fractions that microbes could readily consume, while in Bolmen, stronger light attenuation limited photodegradation, leaving microbial processing as the dominant pathway. These comparisons suggest that while temperature generally enhances bacterial production, the magnitude of seasonal effects depend on the background DOM regime of the system. This pattern is reflected in spectral ratio dynamics, where DOM composition in Bolmen showed relatively stable seasonal responses, while in Erken, spring additions produced sharper shifts consistent with enhanced photodegradation under higher light penetration (Figure 9).

Photochemical processes also vary seasonally. During sunny, low-flow periods, photodegradation decreases DOM aromaticity and produces labile fractions that can be rapidly taken up by microbes. **Paper IV** demonstrated that this effect was strongest in shallow systems during summer, where intense irradiation and warm conditions facilitated the sequential interaction between photochemical breakdown and microbial consumption. In contrast, lower light and cooler conditions during autumn limited these synergistic effects, leaving more aromatic DOM in the system.

Temperature further modulates these dynamics by regulating microbial efficiency. At colder temperatures, enzymatic activity slows, and microbes allocate a larger fraction of consumed carbon to respiration rather than biomass production, leading to lower bacterial growth efficiency (Alonso-Sáez et al., 2008; Berggren et al., 2010). Thus, even labile DOM is used less efficiently in autumn and winter compared to summer.

Taken together, these findings highlight how seasonal shifts in both light and temperature interact with DOM composition to control carbon transformations. Periods of strong irradiation and warm temperatures promote coupled photochemical and microbial processing, while colder, darker seasons favor DOM accumulation and downstream export.

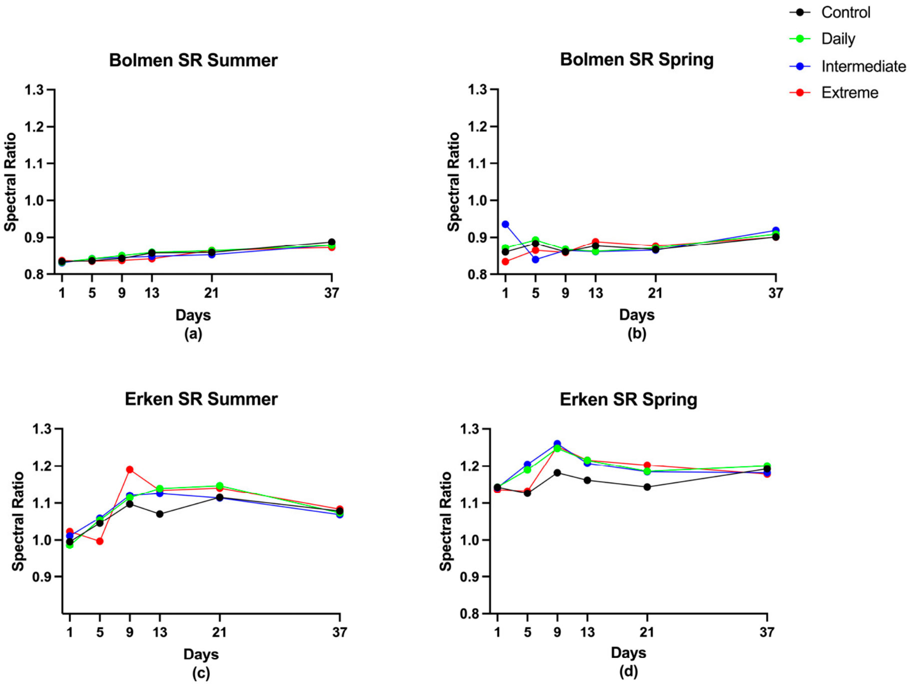

Figure 9. Seasonal DOM processing in Lake Bolmen (humic) and Lake Erken (clearwater) mesocosms. Slope ratio (SR) tracked changes in DOM aromaticity under different addition regimes (control, daily, intermediate, extreme). In Bolmen, SR was stable across seasons, reflecting light limitation and dominance of microbial pathways. In Erken, stronger spring increases in SR indicated greater photodegradation and production of labile DOM fractions for microbial uptake (**Paper III**).

Microbial Carbon Utilization Under Brownification and Eutrophication

Microbial utilization of DOM is strongly influenced by the quality of DOM. The phenomenon of brownification and eutrophication can drastically alter DOM quality and quantity, thereby affecting heterotrophic bacterial metabolism in aquatic systems (**Paper II**). In many northern lakes, these two stressors are occurring simultaneously due to climate and land-use changes. **Paper II** specifically addressed how these forces impact bacterial carbon use.

Brownification typically leads to higher inputs of terrestrial, humic-rich DOM. This DOM is often high in carbon but low in nutrients and yields little energy per unit carbon because of its chemical complexity. As a result, waters undergoing brownification often see low BGE and higher respiration relative to production (Kritzberg et al., 2020). In other words, bacteria in humic-brown lakes tend to respire a large portion of consumed DOM as CO_2 rather than converting it to biomass (Jonsson et al., 2001; Tranvik & Jørgensen, 1995). Studies report BGE declines of roughly 20 – 40 percent in systems dominated by allochthonous DOM, as microbes expend extra energy to break down complex molecules (Berggren & Al-Kharusi, 2020; Berggren et al., 2012). Brownification is thus expected to push aquatic systems toward a more heterotrophic metabolic balance. Consistent with this, **Paper II** showed that adding terrestrial DOM alone caused a sharp increase in bacterial respiration but only a modest increase in biomass production.

Eutrophication, on the other hand, tends to increase autochthonous DOM production. Algal blooms and plant growth release a suite of labile organic compounds (Zhou et al., 2018). Under eutrophic conditions, bacteria often have excess nitrogen and phosphorus to go with the DOM, which means they can utilize carbon more efficiently for growth (higher BGE). In environments with lots of algal DOM, one often observes high bacterial production and relatively lower respiration per unit carbon consumed (Jansson et al., 2006). In **Paper II**, nutrient enrichment alone stimulated bacterial production significantly, while respiration did not respond as strongly. These treatment-level patterns are shown in Figure 10. Mesocosms receiving organic matter (OM) and organic matter + high nitrogen and phosphorous ratio (OM + HNP) exhibited consistently higher BP and BR than both the control and nutrient-only treatments. While the low nitrogen and phosphorous (LNP) and HNP increased BP compared to the control, they remained significantly lower than the OM-containing treatments, highlighting the dominant role of terrestrial DOM in fueling microbial activity. OM and OM + HNP responded very similarly in this short-term experiment, suggesting that immediate stimulation of microbial metabolism was primarily driven by DOM additions. Over longer timescales, however, OM + HNP would be expected to sustain higher microbial turnover due to the combined supply of carbon and nutrients, potentially amplifying CO_2 emissions and oxygen demand at the ecosystem level.

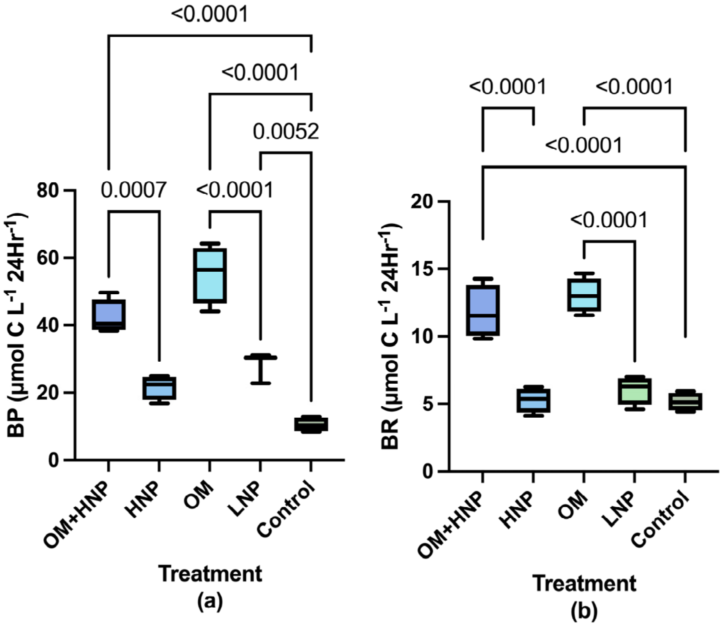

Figure 10. Results from the mesocosm experiment in Lake Bolmen (Paper II), showing BP and BR responses. Treatments: Control = unamended lake water; OM = organic matter additions (soil extract simulating brownification); OM + HNP = combined organic matter and high nitrogen to phosphorus (N:P) ratio nutrient enrichment; LNP = low N:P ratio nutrient enrichment; HNP = high N:P ratio nutrient enrichment.

When brownification and eutrophication co-occur, the interactions can be complex. On one hand, the presence of labile algal DOM (from eutrophication) can stimulate microbes to also degrade humic DOM, a phenomenon known as the priming effect (Guenet et al., 2010). In **Paper II**, combined treatments supported higher bacterial production and respiration compared to brownification alone, and fluorescence data indicated greater microbial utilization of terrestrially derived DOM components. On the other hand, extremely high terrestrial DOM loads can reduce light penetration, which in turn may limit algal production even when nutrients are abundant (Rivera Vasconcelos et al., 2018).

These findings suggest that boreal lakes receiving both elevated DOM and nutrient inputs may shift toward hotspots of microbial activity and carbon flux. The combination of high respiration and high production reflects elevated turnover, with implications for CO_2 emissions and oxygen dynamics explored further in the next section.

Implications for Carbon Cycling and Ecosystem Functioning

Discharge events exported large amounts of terrestrial DOM downstream with limited instream transformation, indicating that hydrology can constrain microbial and photochemical attenuation. These results highlight that catchment-level inputs and transport dynamics are central to whether lakes function as carbon sinks or sources (**Paper I**). The combined influences of brownification and eutrophication, further shaped by seasonal and spatial variation, strongly affect carbon cycling and ecosystem functioning (**Papers II and III**).

Elevated microbial respiration under high DOM conditions contributes to greenhouse gas emissions, particularly CO_2 and potentially CH_4, from inland waters (Bastviken, Cole, et al., 2004). **Paper II** showed that high terrestrial DOM inputs stimulated microbial respiration more strongly than production, shifting metabolism toward net heterotrophy and increasing CO_2 release. When nutrients were also added, both respiration and production increased, but overall CO_2 efflux was still higher**.** This balance is illustrated by BGE patterns in Figure 11. At the initial time point (Figure. 11a), BGE did not differ among treatments, but all treatments were higher than the control, reflecting a general stimulation of biomass production relative to respiration. After a 5-day incubation (Figure. 11b), overall BGE declined and treatment differences became evident: brownification reduced efficiency by favoring respiration, whereas nutrient enrichment maintained comparatively higher efficiency, partially counteracting the decline under humic inputs. **Paper III** further showed that the mode of input also matters. While microbial communities can acclimate to repeated DOM additions, large single pulses may temporarily exceed processing capacity, resulting in sharp oxygen demand that could contribute to transient oxygen stress under natural conditions.

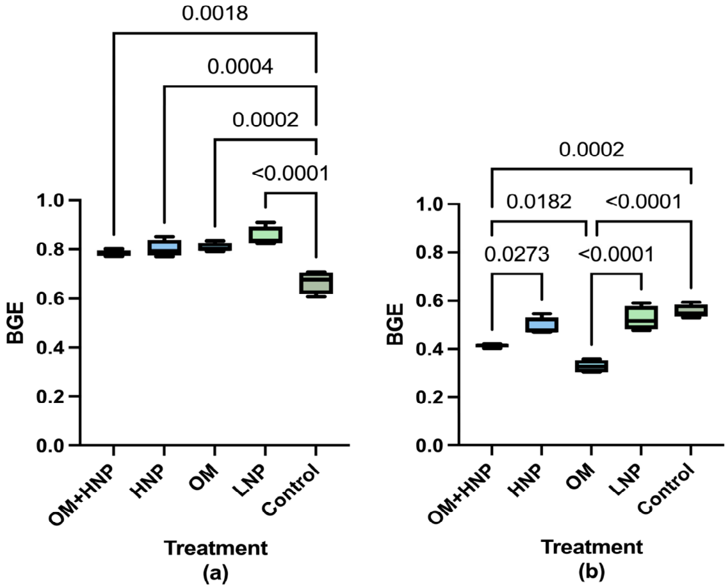

Figure 11. Bacterial growth efficiency (BGE) at (a) the start of the experiment, immediately after treatments were applied, and (b) after a 5-day BOD incubation. At the initial time point, all treatments had higher BGE than the control but did not differ among themselves. After 5 days, overall BGE declined and treatment effects became evident: brownification reduced efficiency, while nutrient enrichment maintained comparatively higher values, partially counteracting the decline under humic inputs (**Paper II**).

Oxygen dynamics and water quality are also affected. In eutrophic systems, microbial uptake of DOM, particularly under high-respiration scenarios, can rapidly consume dissolved oxygen, notably in bottom waters or at night. Brownification can amplify this effect by supplying additional organic substrates that fuel microbial oxygen demand. These oxygen dynamics have additional consequences for nutrient cycling: DOM-driven microbial activity can exacerbate oxygen depletion, which in turn alters nutrient cycling by promoting the release of phosphorus from sediments under anoxic conditions (Carstensen & Conley, 2019; Levin et al., 2009).

The balance between carbon retention and carbon export also shifts under combined stressors. Eutrophication enhances organic carbon retention in microbial and algal biomass, some of which can sediment and be buried. Brownification, by contrast, increases inputs of more refractory humic DOM that is less likely to sediment and more likely to be respired (Kritzberg et al., 2020; Sobek et al., 2007). In **Paper II**, high DOM treatments increased microbial production, but respiration increased as well, meaning the net effect favored CO_2 release over burial. The BGE results reinforce this conclusion by showing that although bacteria initially used carbon more efficiently under treatments, longer incubations revealed that respiration dominated carbon processing under brownification, whereas eutrophication favored greater retention in biomass. At the same time, asynchronous reductions in nitrogen and phosphorus inputs at the catchment scale can shift N:P ratios and thereby alter algal limitation dynamics, with implications for DOM processing and the balance between retention and mineralization (Westphal et al., 2020).

Food web structure and productivity are also influenced. High bacterial uptake of DOM diverts carbon through the microbial loop, which supports bacterivorous zooplankton but can reduce transfer efficiency to higher trophic levels (Anderson & Ducklow, 2001; Elovaara et al., 2021). When respiration dominates compared to growth, much of the carbon is lost as CO_2, further limiting trophic transfer. Brownification also reduces light availability, constraining phytoplankton growth and favoring mixotrophs or heterotrophs.

Taken together, our findings (**Papers I, II, and III**) advance understanding of how microbial communities and carbon pathways respond to multiple stressors. The work demonstrates that predicting a lake's role in the global carbon cycle requires integrating seasonal variability, land use in the catchment, and interactive effects of DOM and nutrients.

Seasonal Carbon Removal Dynamics in Constructed Wetlands

Constructed wetlands (CWs) function as biogeochemical filters, removing or transforming DOM before it reaches downstream waters. Through processes such as photodegradation, microbial degradation, plant uptake, sedimentation, and sorption, CWs have been shown to reduce the export of labile carbon and nutrients from the landscape (Kennedy & Mayer, 2002; Maurice et al., 2022; Overton et al., 2023). Our research (**Paper IV**), supported by **Papers I–III**, examined how CW design and seasonal variation affect DOM removal efficiency, with emphasis on the interplay between photochemical and microbial pathways.

Depth-dependent effects and water residence time (WRT) emerged as key factors controlling DOM transformation. Shallow CWs (~0.3 m depth) received high solar radiation, enabling rapid photodegradation. In our summer trials, this was evident as a decline in specific UV absorbance (SUVA) and a shift toward lower molecular weight, more bioavailable DOM fractions within 1–2 days (**Paper IV)**. In Erken mesocosms (**Paper III**), brief increases in protein-like fluorescence, likely generated through photodegradation of refractory DOM, were subsequently consumed by microbes, highlighting partial rather than complete abiotic–biotic coupling, since some oxidized DOM persisted. This effect was less pronounced in Bolmen. However, shallow systems also exhibited elevated microbial respiration, which consumed oxygen rapidly under high DOM loads. We did not monitor dissolved-oxygen time series in the wetland, but BOD measurements showed faster

O_2 consumption under high DOM additions (**Paper IV**). In natural nutrient-rich systems, such dynamics would be expected to elevate hypoxia risk and, by extension, favor anaerobic pathways (e.g., methanogenesis) as shown for similar systems (Saarela et al., 2022). These patterns are consistent with eutrophication-brownification interactions observed in **Paper II**, where high DOM and nutrient availability jointly elevated respiration and CO_2 production. While nutrient enrichment was not tested in **Paper IV**, results from **Paper II** and prior work suggest nutrients would further amplify respiration.

By contrast, deeper wetlands (~0.6 m depth) showed more gradual but sustained DOM removal. Although UV penetration was reduced, DOM processing showed a more stable balance between photodegradation and microbial activity. Microbial degradation continued even as photochemical transformation declined, and a slower rebound in DOM concentration or aromaticity was observed, unlike in shallow wetlands where recalcitrant DOM sometimes accumulated following rapid initial processing (**Paper IV**). Temperatures were similar between shallow and deep wetlands; the slower DOM transformation in deep systems likely reflected differences in light penetration and microbial processing dynamics, rather than thermal effects. The stable redox conditions in deep systems also appeared to limit the risk of hypoxia, supporting longer-term microbial transformation. Together, these results indicate that shallow systems are characterized by short-lived, light-driven processing, while deeper systems sustain steadier microbial activity. **Paper III**, while not testing depth directly, instead demonstrated that pulse regime and season determined whether microbial processing occurred as short-lived bursts (e.g., extreme treatments) or sustained uptake (e.g., daily additions).

Seasonal dynamics strongly influenced the relative contributions of photodegradation and microbial degradation. In summer, shallow wetlands exhibited pulse-like processing: rapid DOM transformation via photodegradation followed by intense microbial activity. BOD measurements confirmed faster O_2 consumption under high DOM additions in shallow wetlands (**Paper IV**). In deeper wetlands, DOM transformation occurred more gradually, likely due to reduced light penetration rather than differences in temperature. SR and fluorescence data suggested that even in deep zones, photochemical breakdown products were available for microbial use, though **Paper III** showed that such products were not always fully assimilated. When normalized to initial conditions, volume-adjusted TOC trajectories revealed contrasting outcomes between depths and seasons (Figure 12): shallow wetlands rapidly removed carbon but later shifted toward net release, whereas deep wetlands achieved stronger and more sustained net removal. In autumn, both shallow and deep wetlands showed weaker but steadier carbon uptake, with little rebound above baseline (**Paper IV**).

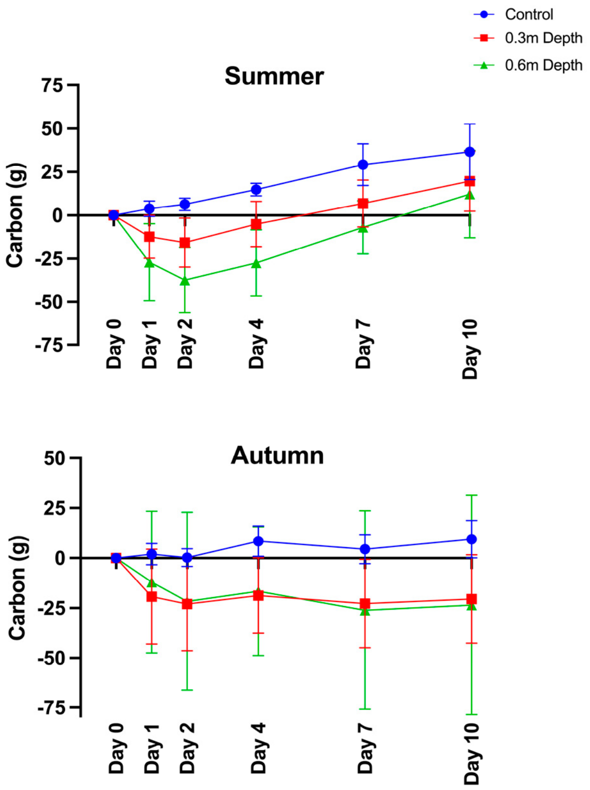

Figure 12. Volume-adjusted TOC (g, normalized to Day 0) over time in shallow (0.3 m) and deep (0.6 m) constructed wetlands compared to controls during June (summer, top) and November (autumn, bottom) trials (**Paper IV**). Values below zero indicate net carbon removal; values above zero indicate net carbon release. Shallow wetlands showed rapid but transient summer removal followed by release, while deep wetlands sustained stronger net removal. In autumn, both depths showed weaker but steadier uptake.

In autumn, lower solar intensity and cooler temperatures shifted the balance further toward microbial degradation. Deep CWs maintained moderate DOM removal, likely due to their ability to buffer temperature declines and provide microbial refugia. Shallow CWs showed greatly reduced photodegradation in autumn; microbial activity persisted but overall DOM-removal rates were lower than in deep CWs (**Paper IV**). These seasonal patterns align with findings from **Paper I**, which identified autumn as a period of elevated terrestrial DOM export from upstream catchments. Our results therefore suggest that deep zones can help mitigate the downstream effects of these pulses even when photochemical activity is reduced.

While spring dynamics were not directly tested, insights from **Paper I** and the broader literature indicate that spring is a critical period for DOM mobilization. Peak discharge events following snowmelt can deliver large amounts of labile DOM to aquatic systems, consistent with the high DOM loads used in the mesocosms and CW trials. Although our data do not directly confirm CW performance in spring, we hypothesize that shallow zones would resume high photodegradation due to increased light, while deeper zones would again support sustained microbial processing. This conceptual model is supported by previous work showing that two-day WRTs in CWs improve DOM attenuation during spring inflows (Xu et al., 2021) and that phototrophic biofilms can facilitate DOM degradation under rewarming conditions (Koehler et al., 2014). Together, this situates wetland function within the seasonal supply context defined by catchment exports (**Paper I**), the microbial processing responses to DOM and nutrient enrichment (**Paper II**), and the microbial use of DOM inputs in lakes (**Paper III**).

Design Implications and Recommendations

The results of this thesis highlight several key considerations for CW design. Multi-depth configurations are particularly effective because shallow and deep zones contribute complementary functions. Shallow compartments maximize photochemical transformation under sunny conditions, whereas deeper zones provide more stable microbial environments that sustain DOM degradation during colder months or low-light periods (Kadlec & Wallace, 2008; Paper IV) (**Paper IV**). Findings from **Paper III** further demonstrate that the balance between photodegradation and microbial processing shifts seasonally with changes in light availability and DOM quality, reinforcing the importance of integrating both shallow and deep zones within a single system. By combining these depth-specific processes, multi-depth CWs can reduce the risk of oxygen depletion and DOM rebound, thereby supporting more consistent year-round performance.

Another important factor is water residence time. A duration of approximately 48 hours proved effective in **Paper IV** and is consistent with previous studies (Wu et al., 2019). Adjustable inlet structures or weirs could provide a practical means of regulating residence time seasonally, slowing throughput during periods of high DOM load while maintaining sufficient flow during lower-load periods.

Maintaining aerobic conditions in deeper zones is also critical. Sustaining oxygen availability prevents shifts to anaerobic pathways, such as methane production, and supports efficient microbial respiration (Mitsch et al., 2013). While not directly measured in **Paper IV**, oxygen management could be achieved through re-aeration features such as small cascades or oxygenation trenches, or by managing DOM loads to avoid excessive depletion before water enters deeper compartments. Pairing BOD and dissolved oxygen monitoring with adaptive design would help preempt hypoxia during high DOM episodes.

Landscape placement also plays a crucial role. Wetlands should be located strategically, guided by the seasonal export pulses identified in **Paper I** and by microbial processing responses to DOM and nutrients described in **Paper II**. The seasonal variation in DOM properties observed in **Paper III** adds further weight to this point, showing that wetland placement and design must account for temporal changes in DOM quality as well as timing of delivery. For example, intercepting spring discharges from forested peat catchments and autumn runoff from agricultural areas could maximize DOM removal before water reaches lakes or coastal systems.

It is important to recognize that CWs represent only one part of the solution. While they are valuable biogeochemical filters, they cannot fully counteract large-scale brownification and eutrophication. Complementary approaches such as reducing external nutrient loading from agriculture, restoring riparian buffers, and adjusting forestry practices that mobilize soil organic carbon will also be required. Importantly, long-term analyses suggest that shallow lake and wetland systems are more often shaped by gradual nutrient-driven trajectories than abrupt regime shifts, underscoring the value of steady, catchment-wide nutrient reduction alongside local CW interventions (Davidson et al., 2023). In this way, CWs should be regarded as one component of an integrated catchment management strategy rather than a standalone solution.

Conclusion

This study demonstrates that photodegradation and microbial degradation are not isolated or mutually exclusive but are interdependent and seasonally modulated. Our data from **Paper IV** underscore the value of multi-depth wetland designs and seasonally appropriate management for reducing DOM loads and mitigating their downstream impacts. These findings contribute to a growing body of evidence supporting constructed wetlands as scalable, adaptive tools for inland water carbon management, while recognizing that complementary catchment-level measures are required to address future increases in brownification and eutrophication. A practical trade-off emerges: shallow light-rich zones rapidly improve watercolor and DOM lability but can elevate oxygen demand; deep zones moderate those risks while sustaining longer-term microbial processing. Future work should assess long-term CW performance under variable hydrological regimes and explore how design flexibility can enhance resilience to increasingly frequent extreme weather events.

Conclusions and Outlook

This thesis contributes new insights into how dissolved organic matter is processed in freshwater ecosystems and how we can mitigate its negative effects. By addressing three key research questions, we have advanced the understanding of DOM transformations, microbial interactions, and wetland-based management strategies. Here, we summarize the novel contributions of this work, discuss its implications for environmental policy, and outline directions for future research.

Novel Contributions

Seasonal and Landscape Controls on DOM Reactivity. We demonstrated (**Paper I**) that the bioavailability of exported DOM peaks during spring and autumn high-flow events and that agricultural catchments supplied DOM with a higher bioavailable fraction, whereas forested catchments exported larger but more refractory DOM pools. Because forest-dominated rivers transport a greater total DOM mass, their cumulative oxygen demand is comparable to that of agricultural rivers. Effective management therefore requires concurrent measures in both landscape types and must include autumn as well as spring. This result provides quantitative support for the concept that timing and source jointly determine the ecological impact of dissolved organic carbon. These patterns can be interpreted considering the intrinsic and extrinsic controls described earlier, whereby chemical composition influences lability and physical context such as hydrology and light regimes constrain the extent to which DOM is processed once exported.

Interactive Effects of Brownification and Eutrophication. An in-lake mesocosm experiment (**Paper II**) showed that simultaneous additions of terrestrial DOM and inorganic nutrients produced responses not observed when each stressor acted alone. Nutrient enrichment approximately doubled bacterial production and elevated respiration relative to the DOM-only treatment, indicating that added nitrogen and phosphorus relieved metabolic constraints and enhanced utilization of humic substrates. Although a larger fraction of carbon was channeled into microbial biomass, cumulative respiration and thus CO_2 efflux also exceeded that of the DOM-only mesocosms. These results demonstrate that lake carbon processing is jointly regulated by nutrient status and DOM supply: mitigation of browning impacts will therefore be more effective when coupled with nutrient-load reductions to avoid amplifying heterotrophic CO_2 emissions.

DOM Input Regimes and System Memory. In two lake systems subjected to contrasting DOM-loading regimes (**Paper III**), lakes with historically low DOM exhibited slower initial processing of an abrupt input. Responses to repeated pulses were variable, with some evidence of microbial adjustment but not a consistent increase in efficiency. In the humic lake, a second pulse did not markedly increase processing, suggesting that acclimation is constrained when baseline DOM concentrations are already high. The impact of DOM additions depends not only on their amount and composition but also on whether they occur gradually or as discrete pulses. These findings indicate that while microbial communities can adjust to repeated inputs, large single events may temporarily exceed processing capacity and induce transient oxygen stress.

Optimizing Constructed Wetlands for DOM Removal. **Paper IV** shows that shallow wetland zones favor photochemical transformation and deeper zones sustain microbial degradation, implying that a sequential shallow-plus-deep configuration could extend the range of conditions under which DOM removal is optimized. Although this study did not test a series arrangement, the depth-specific efficiencies provide a mechanistic basis for future design trials. The experiment further demonstrated that prolonged residence times in shallow CWs can promote secondary formation of humic-like DOM late in the season, indicating that retention time must be balanced against the risk of re-export. These findings augment existing wetland design guidelines traditionally focused primarily on nutrient removal by introducing quantitative considerations for carbon management.

Policy and Management Implications:

Mitigating coastal hypoxia and brownification

Baltic Sea action plans, particularly HELCOM's Nutrient Input Reduction Scheme, aim to reduce both nutrient and organic matter inputs that sustain oxygen depletion and watercolor deterioration. The findings of this thesis indicate that simultaneous reductions in nutrient runoff and DOM export are essential; tackling either stressor alone is unlikely to break the heterotrophic oxygen-demand cycle. Integrated watershed measures such as riparian buffer strips, targeted reforestation, and stricter fertilizer caps should therefore be framed as a single policy package rather than separate initiatives.

Timing of management actions

Spring snowmelt and autumn storm flows transport the most bioavailable DOM. Season-specific interventions, for example brief increases in reservoir residence time during melt or storm windows, could enhance natural photochemical and microbial processing before water reaches downstream systems. These schedules align with existing seasonal restrictions that protect spawning fish and thus require minimal additional regulation.

Constructed wetlands and other nature-based solutions

Depth-stratified wetlands remove both nutrients and carbon. Cost–benefit analyses can factor in savings on downstream drinking-water treatment as well as the climate-regulation value of reduced carbon export. Design guidelines should stipulate that at least 30 percent of the wetland area is shallower than 0.5 m to maximize photochemical breakdown, paired with deeper areas that sustain microbial degradation. These criteria could be written into agri-environment programs that compensate landowners for multifunctional wetlands.

Adapting to climate change

Projected increases in winter runoff and episodic storms will raise DOM loads. Networks of shallow-plus-deep wetlands and reconnected floodplains can buffer these pulses hydraulically while limiting downstream DOM transfer. Because warmer water enhances respiration and methane production, climate-smart planning should pair wetland expansion with complementary carbon-offset options, such as promoting sediment carbon burial or managing drawdowns to minimize ebullitive methane releases.

Future Research Directions

Future research should address long-term and large-scale responses through whole-lake manipulations and watershed-gradient studies, which are needed to test whether the DOM–nutrient interactions observed here persist under chronic exposure and how microbial communities shift carbon budgets over time. Such studies will also test whether the processes identified in **Papers I–IV** scale up to landscape-level carbon budgets. At the same time, mechanistic microbial ecology approaches such as metagenomics, transcriptomics, and targeted enzyme assays can identify the taxa and pathways that govern humic degradation and processes such as priming. These approaches can also help clarify whether microbial acclimation to repeated DOM inputs has an upper limit, particularly under intensifying brownification. A further priority is to develop complete greenhouse-gas budgets by pairing DOM removal measurements with high-resolution CO_2 and CH_4 fluxes, including both diffusive and ebullitive CH_4 fluxes during drawdown, to determine the net climate impact of carbon-oriented wetland designs. Extreme events, including drought–rewet cycles or storm pulses, also warrant attention, since experiments simulating these conditions can reveal how rapidly wetlands and lakes recover DOM-processing capacity and whether repeated disturbances cause cumulative impairment. Finally, integrating these processes into catchment and lake models will allow for regional forecasts and virtual management scenarios, for example by testing the effect of converting portions of a watershed to wetlands.

This thesis demonstrates that water quality, carbon cycling, and climate feedback are linked through dissolved organic matter. By combining mechanistic insights with applied measures such as depth-optimized wetlands, this work provides a process-based foundation for managing DOM under changing climate and land use. Protecting freshwater ecosystems and the services they provide will require continued collaboration across disciplines, and the integrated approach developed here can serve as a template for addressing other complex environmental challenges that span multiple processes and scales.

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Acknowledgements

First and foremost, I would like to express my deepest gratitude to **Johanna Sjöstedt**. You have been the most outstanding supervisor I could ever hope for, and I am truly grateful for the attention, care, and hard work you have invested in me over the past six years. Your ability to balance sharp scientific thinking with encouragement and patience has shaped me not only as a researcher but also as a teacher and colleague. I greatly appreciate your generosity with your time and feedback, your trust in allowing me to develop independently, and your guidance in navigating both challenges and successes. Working with you has been a privilege, and your influence will continue to guide me long after this thesis.

I wish to thank my co-supervisors **Martin Berggren**, **Lettice Hicks**, and **Anders Persson**. Thank you, Martin, for your expert advice on content specific details.

I am grateful to my departmental representative, **Johannes Rousk**, for his engaged supervision and many valuable conversations. It has been a real pleasure to work with you in this role.

I would also like to thank the former **Aquatic Ecology department** for all the great coffee breaks and conversations over the years. Those small moments of light-heartedness lifted the stress of research, and they also created space to bounce ideas off colleagues, often helping me clarify concepts and find new perspectives.

To all my **collaborators** and **co-authors**, thank you for the stimulating discussions, shared fieldwork challenges, and constructive comments on manuscripts. A special thanks goes to **SITES** (Swedish Infrastructure for Ecosystem Science) for allowing me to use their infrastructure and for the support provided by everyone involved. It was a privilege to be part of such a multinational and multidisciplinary experiment.

To my colleagues in Halmstad, **Antonia**, **Jasmine**, and **Josephine**, thank you for the great collaboration and the fun times we shared out in the field. **Juha Rankinen**, I am especially grateful for all your hard work at Bolmen; we could not have done it without you. I also wish to thank **Kristianstad Vattenrike** for allowing us to use parts of their infrastructure and for providing a space to hold meetings and share results with fellow researchers and stakeholders.

I am especially grateful to **Kathleen Murphy** for teaching me PARAFAC and for generously allowing me to use your Aqualog during the difficult circumstances of the pandemic. I also want to thank the gang at DTU Aqua, especially **Colin**

Stedmon and **Urban Wünsch**, for further teaching me PARAFAC and welcoming me into your lab space. It was a privilege to learn from you, and those experiences greatly shaped my work.

I would also like to thank all my former **master's students** for their help and for all the great times in the lab and field. Working with you was both rewarding and fun, and your contributions meant a lot along the way.

I also want to thank my fellow **PhD students** for the camaraderie, support, and good times we shared throughout this journey. From long days in the lab and field to conferences, and after-work gatherings, your company made the PhD years both enjoyable and memorable. The sense of community we built helped me navigate the ups and downs of research, and I am grateful to have shared this time with you. Special thanks to **Flavio** for all the shenanigans and side quests we ended up going down. They made the journey much more enjoyable.

Finally, I would like to thank my wife **Emma**, my daughter **Nora**, and our dogs **Edna** and **Ester** for their love and support. More importantly, thank you for keeping me so busy at home that I had less time to stress about work. Your presence has given me balance, joy, and perspective throughout this journey, and this thesis would not have been possible without you.

Printed by Media-Tryck, Lund 2025 NORDIC SWAN ECOLABEL 3041 0903

List of Papers

I. Jones, K., Berggren, M., & Sjöstedt, J. (2023). Seasonal variation and importance of catchment area composition for transport of bioavailable carbon to the Baltic Sea. Biogeochemistry. https://doi.org/10.1007/s10533-023-01079-y

II. Jones, K., Liess, A., & Sjöstedt, J. (2024). Microbial carbon utilization in a boreal lake under the combined pressures of brownification and eutrophication: insights from a field experiment. Hydrobiologia. https://doi.org/10.1007/s10750-024-05718-9

III. Jones, K., Sjöstedt, J., Berggren, M., Liess, A., Borgert, J., van Dam, E., Oppong, J. C., Nejstgaard, J. C., Pedregal, A., Catalán, N., Lupon, A., Perujo, N., Charmpila, E. A., Langenheder, S., Kulaš, A., Bernal, S., Bick, B., Berger, S. A., & Yaqoob, M. (2025). CDOM and nutrient pulse variability influence DOM characteristics and microbial responses in experimental boreal lake systems. *Manuscript*.

IV. Jones, K., Borgert, J., van Dam, E., Liess, A., & Sjöstedt, J. (2025). *Depth and water residence time shape dissolved organic matter removal in constructed wetlands*. [Manuscript in revision, Journal of Environmental Management.]

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ISBN 978-91-8104-701-1

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