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Phytoplankton in humic and colored Nordic lakes

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Lake Vansjø, Norway. Photo: Camilla Hedlund Corneliussen Hagman

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Preface

This report is written as a special syllabus during a PhD program at the Faculty of Environmental Sciences and Natural Resource Management. The topic was mainly focused on lakes in Nordic countries. Practically, this meant mainly Sweden and Finland, where most studies on phytoplankton in humic lakes have been published.

The author is aware that the Raphidophyte *Gonyostomum semen* is a common species in Nordic, humic lakes. However, since this species is the topic of the author's PhD thesis, the current report was mainly focused on other taxonomic groups.

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Camilla H. Corneliussen Hagman

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Summary

Concentrations of lake dissolved organic carbon (DOC) transported from catchments, with simultaneous browning, are currently increasing in boreal lakes, and predicted to continue in the future. This increased load of organic matter has several complex effects on lake physiology and chemistry. The most prominent effect in lakes is reduced light availability, which is the main driver for photosynthesis and lake primary production. This report is a review of the most significant effects from increased DOC and browning, and how these affect the phytoplankton community and shape the assembly of taxonomic groups in these lakes. The report is focused on Nordic lakes, in which the Raphidophyte *Gonyostomum semen* is not present or dominating. These humic lakes are mainly inhabited and dominated by species of Cryptophyta, Chrysophyceae and Bacillariophyceae (diatoms). Several lakes also have significant amounts of Dinophyta (dinoflagellates) while presence of Chlorophyta (green algae) is only occasionally pronounced. The common, and apparently beneficial traits of species in humic lakes, are the ability to adjust their position according to light availability, including vertical migration, as well as having the pigment composition that maximizes absorption of the available light. Some species are also mixotrophic, which is an advantage in reduced light conditions, where they instead may have better availability of organic energy sources. Several species are well adapted to conditions provided by high DOC concentrations and dark lake color. Still, they are likely to live under suboptimal conditions. It may therefore be, that the reason for their dominance in these lakes is in fact the lack of this ability or adaptation in other species.

Norsk sammendrag

Konsentrasjonen av løst organisk karbon (dissolved organic carbon - DOC) transportert fra nedbørfelt øker sammen med farge i boreale innsjøer, og dette forutsies å fortsette fremover. Denne økte belastningen med organisk materiale har flere og komplekse effekter på innsjøenes fysiologiske og kjemiske forhold. Den mest fremtredende effekten i innsjøer er redusert lystilgjengelighet, som er den viktigste drivkraften for fotosyntese og primærproduksjon i innsjøer. Denne rapporten er en gjennomgang av de viktigste effektene på planteplanktonsamfunn ved økt DOC og farge i nordiske innsjøer, og hvordan disse effektene kan påvirke sammensetningen av taksonomiske grupper. Humøse innsjøer er hovedsakelig dominert av arter av algegruppene Cryptophyta, Chrysophyceae og Bacillariophyceae (kiselalger). Flere innsjøer også har betydelige mengder Dinophyta (dinoflagellater), mens det mer sjeldent er dominerende mengder Chlorophyta (grønnalger). Gruppene som finnes i slike innsjøer har til felles at de ofte er mobile, i tillegg til at mange utfører vertikal vandring, dermed kan de justere posisjon i forhold til lysmengde i vannsøylen. Andre felles egenskaper er en pigmentsammensetning som maksimerer absorpsjonen av det tilgjengelige lyset, samt evnen til benyttelse av alternative energikilder ved mangel på lys. I humøse sjøer vil disse algene ha bedre tilgjengelighet av organisk materiale, samtidig som bakteriebiomassen ofte øker. Flere arter er godt tilpasset forholdene ved høye DOC-konsentrasjoner og mørk innsjøfarge. Likevel lever de sannsynligvis under suboptimale forhold. Derfor kan årsaken til deres dominans i disse innsjøene faktisk være andre arters mangel på slike egenskaper, og ikke nødvendigvis deres egen overlegenhet.

Introduction

Humic and colored lakes, which are simultaneously acidic, are common lake types in Scandinavia as a result of forests, swamps and mires dominating the catchment areas (Maileht et al. 2013). Contrary, southern European lakes are in general clearer and less humic than lakes in Northern Europe (Nõges 2009). Humic refers to the concentrations of humic substances (HS), which are usually the main constituents of lake dissolved organic carbon (DOC) (Tranvik and von Wachenfeldt 2009), and which also contributes dark color (Wetzel 2001). Hence, DOC and water color are often correlated (Kritzberg 2017, Škerlep et al. 2020).

The proportion of DOC that can absorb solar radiation, namely chromophoric dissolved organic matter (CDOM), is a major constituent of total DOC (Wetzel 2001). CDOM contributes color to the water, and consists of chromophores, molecular components that absorb UV and solar radiation > 290 nm (Wetzel 2001). However, the final effect on lake color depends on the quality and composition of the DOC, which again depends on the nature of the catchment area. In some boreal lakes and rivers, water color is also driven by Iron (Fe) concentrations (Kritzberg and Ekström 2012, Xiao et al. 2013, Weyhenmeyer et al. 2014).

> «The organic matter of soils and waters can be viewed as a mixture of plant, microbial and animal products in various stages of decomposition…”
>
> Wetzel 2001

DOC is the major part of total organic carbon (TOC) and dissolved organic matter (DOM) exported into lakes from their catchments (allochthonous origin) (Thurman 1985a, Tranvik and von Wachenfeldt 2009). This organic matter derives from decomposed plant material and soil (Thurman 1985b, Wetzel 2001), hence soil type and quality, land cover, catchment geology and forest composition are important for the quantity, quality and properties of the DOC (Thurman 1985b, Sepp et al. 2019). Some DOC is also produced in the lake itself (autochthonous origin), by decomposition of organic material such as algal and animal cells, however in most lakes this only makes up a minor fraction of the total lake DOC (Thurman 1985b, Wetzel 2001). Organic matter, especially allochthonous, consists mainly of humic substances, since the non-humic substances are labile and easily utilized, and therefore usually only found in low concentrations in the water (Wetzel 2001, Tranvik and von Wachenfeldt 2009). Humic acids, fulvic acids and humin together form the humic substances, and their molecular weight and functional groups determine their adsorption properties, light absorption efficiency and metal binding characteristics ((Wetzel 2001) and references therein).

It is important to distinguish between certain lake types and their properties, as their response to increased DOC and browning may not be similar. A majority of Nordic lakes are located in forested areas, thus they are often humic and nutrient-poor (Maileht et al. 2013). Lakes that are high in

DOC and water color may still have a relatively large secchi-depth, if they are unproductive and have low turbidity. Contrary, what is defined as clear lakes due to low DOC concentrations and water color, may be nutrient-rich and consequently have high productivity. In these lakes, large biomasses of algae can cause high turbidity and reduced secchi-depths, and also alter the water color of the lakes (Thurman 1985b). Further, DOC content and water color depend not only on catchment properties, but also on lake depth, and size in relation to catchment size. For instance, lakes with large volumes and small catchment areas will mostly be clear. This is due to a small area from which inputs of DOC derives, and longer residence time in the lake for the DOC to settle out of the water phase. At the opposite end are small, shallow lakes, with large catchments. These have large amounts of DOC transported into the lake, and less time for the organic matter to settle, thus they will be more colored. Finally, of course variability between these extremes is substantial, and exceptions caused by other factors. Figure 1 shows lake Vansjø, which is a rather large lake in South-East Norway, however with several narrow and shallow basins. The large catchment area is covered in both forest and agricultural land, and the lake is both humic and nutrient-rich, with high productivity (Skarbøvik et al. 2019). During spring 2020 the lake was exceptionally humic for a long period.

Figure 1. Borgebunn basin, Lake Vansjø 20.04.2020. Photo: Camilla H. Corneliussen Hagman

One of the most pronounced changes in boreal lakes that occurred during the past decades, or possibly the past century, is the increased inputs of terrestrial DOC, with subsequent increases in water color of lakes and rivers (browning), especially in forested areas. This trend has been confirmed by several studies in Nordic countries, especially since the 1980s (Hongve et al. 2004, de Wit et al. 2007, Monteith et al. 2007, Finstad et al. 2016, Riise et al. 2018). The causes are not uniform or consistent, but several factors contribute. While some drivers are important for short-term variation, other factors may be important in the long-term (Škerlep et al. 2020). Also, the causes again depend on lake morphology and size, catchment properties and climatic factors. The recent recovery from acidification has driven the increased inputs of organic matter into boreal lakes since the 1980s (Hongve et al. 2004, de Wit et al. 2007, Monteith et al. 2007, Finstad et al. 2016, Riise et al. 2018).

However, other local factors have also proven important, such as afforestation (Kritzberg 2017, Xiao et al. 2020), land cover and agricultural changes in the catchment (Weyhenmeyer et al. 2016, Xiao et al. 2020), as well as regional factors such as increases in temperatures and precipitation (Hongve et al. 2004, Haaland et al. 2010, Xiao et al. 2020). Since these are all ongoing changes, browning is likely to continue to increase in the future, which is also predicted by several models (de Wit et al. 2016, Weyhenmeyer et al. 2016). Such increases in organic matter loads to boreal lakes have impacts on the physical and chemical environments of these lakes, and have further consequences for biota.

This report is a review of the most important lake responses following increased DOC and browning, with a focus on consequences for the typical phytoplankton communities in humic, Nordic lakes. Descriptions of the major dominating groups are included, in order to reveal eventual similarities and traits that are of competitive advantage in humic conditions. The purpose of this paper is to get an overview over how increased DOC and browning may influence and alter Nordic phytoplankton communities in the future.

Effects of increased lake DOC and water color

Physical effects

Light attenuation

DOC has many, and complex effects on lake physiochemistry. The effects are depending on the quality and structure of the DOC, but also on the morphology and properties of the lakes and catchments. Increasing levels of DOC transported from the catchments, most obviously result in increasing lake color, towards yellow-brown or even darker. The humic substances that are components of DOC, have brown color, and consist of acidic functional groups and aromatic structures, chromophores, which absorb UV and short wavelength radiation (Tranvik and von Wachenfeldt 2009). The degree of color of DOC is dependent on the molecular weight of these chromophores, however Fe will also impact the chromophoric properties of DOC, intensifying the brown color (Creed et al. 2018). Figure 2 shows how different water color can be in lakes due to DOC and Fe within a close proximity (distance of 35 km).

Figure 2. Water color due to organic matter and iron, sampled from six lakes in Southern Sweden within a distance of 35 km. Photo: Stefan Löfgren.

When DOC concentrations increase, solar radiation will, after reaching the water surface, be absorbed faster by the increased amounts of chromophores, thus light availability decreases. DOC mainly absorbs short wavelengths of light, hence attenuation is strongest in the blue part of the photosynthetic active radiation (PAR) spectrum, followed by the green region (Jones 1998, Tranvik and von Wachenfeldt 2009). These are the regions of wavelengths also mainly absorbed by photosynthetic and light harvesting pigments such as chlorophylls and carotenoids (Kirk 1983), i.e. the wavelengths mainly used for photosynthesis. For this reason, clear, ultraoligotrophic lakes will be dominated by blue/green irradiance, while moderately colored lakes will be green-dominated, and highly colored lakes will be red-dominated (Jones 1998).

Thermal stratification

In dark colored lakes, the red and infrared dominated surface layers will become heated, while the absorption of solar radiation prevent heat from reaching deeper layers (Longhi and Beisner 2009, Read and Rose 2013). Consequently, the volume of the cold-water hypolimnion increases, while greater temperature differences develop between the layers, promoting a more stable thermal stratification compared to that of clearer lakes (Houser 2006, Longhi and Beisner 2009, Read and Rose 2013). Also, studies have found epilimnion temperatures to be colder in colored lakes (Houser 2006), which overall may create lower water temperatures in humic lakes (Read and Rose 2013). As a further consequence of this rapid absorption of solar radiation below the lake surface, humic lakes have shallower thermoclines and epilimnion depths, which again restricts the photic zone, where photosynthesis is possible (Jones 1998, Klug and Cottingham 2001, Houser 2006, Longhi and Beisner 2009, Read and Rose 2013, Strock et al. 2017). In humic lakes, the photic zone is therefore often shallower than the epilimnion depth. These responses to increased DOC concentrations will be more pronounced in deeper lakes compared to shallow lakes, even with similar DOC levels. This is because, when the depth of the epilimnion and photic zone decreases, the proportion of the total lake volume that will be suitable for primary production will be even less in deeper lakes than in shallow lakes (Seekell et al. 2015). Due to increased hypolimnion volumes and the increased resistance to mixing when DOC concentrations increase, bacterial consumption of organic matter may increase, and as a consequence may even promote anoxic hypolimnetic conditions (Nürnberg and Shaw 1998).

Chemical effects

Alkalinity and contaminants

The acidic functional groups of humic substances affect the acid-base chemistry of freshwaters, and as a consequence, DOC-rich lakes are often slightly acidic (Klug and Cottingham 2001, Tranvik and von Wachenfeldt 2009). Also, in addition to influencing light availability and temperature, the absorption of solar radiation by the aromatic structures of humic substances results in photochemical reactions. These reactions alter the fate of metals and organic pollutants, for instance they increase solubility of hydrophobic compounds such as pesticides (Tranvik and von Wachenfeldt 2009). At low alkalinity, as is the case for many humic lakes, hydrophobic contaminants such as poly-chlorinated biphenyls (PCB) are increasingly bound to DOC, and consequently less available for uptake in organisms (Tranvik and von Wachenfeldt 2009). Also, the bioavailability of certain toxic compounds, trace metals and toxic metals is affected by binding to DOC. Hence, DOC is regulating the mobility of metals in aquatic environments, which may be either beneficial or inhibiting for phytoplankton (Jones 1998, Tranvik and von Wachenfeldt 2009, Creed et al. 2018). A recent study showed that low DOC concentrations (5 mg C L^{-1}) together with pH positively influenced the ability of algae to adapt to certain micropollutants, reducing their toxic effect on the adapted populations. However, this effect vanished at higher DOC levels (15 mg C L^{-1}) (Rizzuto et al. 2020). Hence, higher DOC levels may prevent necessary tolerance acquisition for algal communities exposed to contaminants (Rizzuto et al. 2020).

Nutrients

It is inevitable that DOC affects the nutrient conditions for phytoplankton, in one way or another, by being a potential source of carbon and energy for some species, and also by changing the bioavailability of essential elements (Jones 1998). In addition, the actual stoichometric requirements of nutrients in algal cells may also be affected by changes in light availability, altering the necessary N:P pool for phytoplankton growth (Thrane et al. 2016). DOC with its humic substances contain significant amounts of nitrogen (N) and phosphorus (P), consisting of mainly organic fractions (Tranvik and von Wachenfeldt 2009). These organic nutrients are initially unavailable for primary producers, however through mineralization into inorganic nutrients by for instance solar UV radiation or bacterial action, bioavailable inorganic N and P is produced ((Vähätalo et al. 2003, Tranvik and von Wachenfeldt 2009, Feuchtmayr et al. 2019) and references therein). Yet, the summed effect of DOC on phytoplankton with regards to nutrients is still unclear, and studies contradictory. Nürnberg and Shaw (1998) found no indication that nutrient limitation differs between humic and clear water lakes. Contrary, Isles et al. (2020) found a pattern of decreasing dissolved inorganic nitrogen (DIN) to total phosphorous (TP) relationship with increasing DOC. This would indicate that N-limitation and not P-limitation becomes dominating in increasing humic conditions (Isles et al. 2020), and is supported by other studies on fertilization in clear and humic lakes, where N-limitation was evident in DOC-rich conditions (Jansson et al. 2001). The N-limitation may be a result of total nitrogen (TN) being less available to phytoplankton than TP, or that DOC contributed higher inputs of P into the lake (Isles et al.

2020). Isles et al. (2020) found inter-site differences in their results, which may be related to the composition and the origin of the DOC (Thurman 1985b). In some lakes, when bacterial growth is promoted by increased DOC, they may also outcompete phytoplankton for the available nutrients, thus reducing algae growth (Klug 2005).

Iron (Fe) is the most important trace component for algal cells, and it is occasionally limiting for phytoplankton photosynthesis (Reynolds 2006, Tranvik and von Wachenfeldt 2009). Total Fe is often present in significant amounts in fresh waters (Reynolds 2006). However, it is mostly bound to particles and therefore unavailable for algae, and also rapidly settling out of the water column (Reynolds 2006). Humic matter acts as necessary chelating ligands, and consequently Fe(III) stays in solution by forming complexes with DOC, increasing its availability for phytoplankton (Reynolds 2006, Tranvik and von Wachenfeldt 2009). The need for Fe might also depend on light availability, as Fe is an important component of chloroplasts ((Reynolds 2006, Schoffman et al. 2016) and references therein). When subject to low light intensities, as in humic waters, algae will increase their number of chloroplasts in order to compensate for reduced light, which is a process requiring large amounts of Fe (Schoffman et al. 2016). Hence, at suboptimal light intensities, increasing concentrations of Fe will be required (Schoffman et al. (2016) and references therein).

When oxygen is present, especially in acidic conditions, stable colloids are formed between humic substances, Fe(III) and inorganic phosphorous, whereupon P becomes unavailable for uptake by phytoplankton (Søndergaard et al. 2003, Tranvik and von Wachenfeldt 2009). Contrary, in anoxic hypolimnetic conditions, which may be the situation in stratified lakes, Fe(III) is reduced to Fe(II) and both Fe and P is released from the colloids and into solution (Søndergaard et al. 2003). This is the mechanism of internal P-loading from the sediments back into the water, which is therefore likely to increase in humic, stratified lakes. In nutrient poor and P-limited lakes, this may be of great advantage to phytoplankton, especially species which are able to reside in the hypolimnion.

Effects on lake primary productivity

DOC affects phytoplankton directly and indirectly by changing physical and chemical lake conditions. Direct effects are caused by increased nutrient levels, and alteration of the light environment (Jones 1998). Indirect effects are caused by the impact on thermal structure and stability of stratification of the water column, in addition to changes in euphotic and epilimnetic depths, hence consequences that are caused by DOC absorbing heat and light radiance (Jones 1998).

Solar radiation is the main energy source and driver for whole lake primary production in northern lakes (Wetzel 2001, Seekell et al. 2015), and also important for the response of phytoplankton to other stressors (Klug and Cottingham 2001). Contrary, benthic primary production may be greater than pelagic in some humic lakes (Seekell et al. 2015, Vesterinen et al. 2016). Several northern lakes are shallow and pelagic zones are dominated by the littoral zone areas (Wetzel 2001). Hence, benthic primary production may be of great importance in these lakes, however it is not the focus here.

Long-term decreases in primary productivity has been correlated to browning and increases in DOC ((Kankaala et al. 2019) and references therein). This lower pelagic primary production is a consequence of reduced light availability from increased DOC (Thrane et al. 2014, Deininger et al. 2017). In addition to a reduction in primary production, humic lakes often have higher rates of bacterial biomass and production in relation to phytoplankton biomass and production (Nürnberg and Shaw 1998, Jansson et al. 2000). Hence, increasing DOC concentrations in lakes are potentially causing a shift from a net productive to a net heterotrophic state, especially in the pelagic (Jansson et al. 2000). Effects on lake primary production and phytoplankton biomass caused by changes in DOC levels are, however, dependent on several factors. First, the initial trophic state of the lake, including DOC concentrations are important. In clear lakes, DOC additions may actually protect algae cells from harmful UV radiation by absorbing these short wavelengths (Jones 1998). However, when DOC concentrations and lake color become too high, phytoplankton may instead become light limited (Jones 1998).

In moderately humic conditions, when color is below 100 mg Pt L^{-1}, and DOC concentrations not much higher than 10 mg C L^{-1}, phytoplankton biomass and primary production may be high (Maileht et al. 2013, Bergstrom and Karlsson 2019, Feuchtmayr et al. 2019). Enrichment of mineral nutrients along with the humic matter might promote algae growth in these conditions (Maileht et al. 2013). In fact, several studies found enhanced effects on phytoplankton biomass, or primary production, with increasing DOC concentrations up to a threshold of 10 (Feuchtmayr et al. 2019) to 11 (Bergstrom and Karlsson 2019) mg C L^{-1}. Also, this threshold causes a shift from autotrophy towards chemotrophy, reducing primary productivity (Jansson et al. 2000). When comparing phytoplankton biomass in a clear lake to a humic lake with mean DOC concentrations < 10 mg C L^{-1}, Holopainen et al. (2003) found twice the amount in the humic lake. These lakes were both low with regards to production, however the humic lake had higher concentrations of both TP and TN, indicating that nutrients, rather than light were limiting in these conditions. Similarly, additions of nutrients does not have as positive effect on primary production as expected when DOC concentrations are high, compared to effects observed in clear lakes (Arvola et al. 1996, Seekell et al. 2015, Deininger et al. 2017, Bergstrom and Karlsson 2019, Feuchtmayr et al. 2019). Hence, in lakes with higher DOC levels and darker color, light attenuation becomes dominating, and if light limited, phytoplankton cannot respond to increases in nutrients (Klug and Cottingham 2001). Contrary, Faithfull et al. (2015) found during a mesocosm study that the decreases in primary productivity due to reduced light availability, was actually greater in originally clear waters than in already humic waters. This indicates that the phytoplankton community present in these humic lakes may already have been adapted to low light availability and had a higher threshold for DOC tolerance. Thus, initial state of the lake and composition of the phytoplankton community is determining the responses of increased DOC and browning.

Phytoplankton assemblies in humic lakes

The species composition and functional groups that make up the phytoplankton community in a given lake, is determined by several factors in the lake itself, as well as catchment properties and climate. In Europe, water color, alkalinity and total phosphorus (TP), as well as latitude, are the main factors determining which phytoplankton taxa dominate (Maileht et al. 2013). As lake DOC influences both water color and alkalinity, and depends on latitude (Nõges 2009), this parameter is a major driver for the composition of phytoplankton in Nordic countries.

Humic and dark boreal lakes are typically dominated by few species (e.g. (Holopainen et al. 2003, Willén 2003)). Due to the reduced light conditions, is the ability to adjust their location towards better light conditions, or the ability to utilize other energy sources than solar radiation, of great advantage in dark colored lakes. Thus, species inhabiting humic lakes are mainly motile and often mixotrophic (Drakare et al. 2003, Peltomaa and Ojala 2010). However, other effects from increases in DOC, such as reduced pH and the remaining wavelengths of light, will also prevent the presence or restrict growth of certain algae species (Jones 1998, Klug and Cottingham 2001), and therefore shape the community. Consequently, phytoplankton communities in humic lakes usually have large similarities. Frequently dominating algae groups in humic, boreal lakes are Cryptophyta (Rask et al. 1986, Lepistö and Rosenström 1998, Lepistö et al. 2004, Haande et al. 2012, Maileht et al. 2013, Deininger et al. 2017), Chrysophyta (Rask et al. 1986, Lepistö and Rosenström 1998, Holopainen et al. 2003, Lepistö et al. 2004, Haande et al. 2012, Maileht et al. 2013) as well as diatoms (Bacillariophyceae) (Lepistö and Rosenström 1998, Lepistö et al. 2004, Haande et al. 2012, Maileht et al. 2013), and also, but less frequently, dinoflagellates (Dinophyta) and green algae (Chlorophyta) (Rask et al. 1986, Drakare et al. 2002, Holopainen et al. 2003, Peltomaa and Ojala 2010, Haande et al. 2012).

Figure 3. Lake Kroktjern, South-East Norway, is a small, extremely dark colored lake (> 250 mg Pt L^{-1}*) surrounded by forest. At sampling during summer 2018, the phytoplankton community was dominated by* Synura *sp. Photo: Camilla H. Corneliussen Hagman*

These algae groups may dominate at different times during the growth season, and the composition varies between lakes (Rask et al. 1986, Wetzel 2001, Holopainen et al. 2003, Haande et al. 2012). Cyanobacteria are common in several temperate humic lakes, and also expected to increase with browning and increased DOC concentrations, possibly with more frequent toxin-producing populations (Longhi and Beisner 2009, Creed et al. 2018, Feuchtmayr et al. 2019). However, their abundance in Nordic humic lakes is scarce (Rask et al. 1986, Lepistö and Rosenström 1998, Lepistö et al. 2004, Haande et al. 2012, Maileht et al. 2013, Deininger et al. 2017). The flagellated group Raphidophyceae, and mainly *Gonyostomum semen*, is often and increasingly dominating Nordic humic and colored lakes (Bjørndalen and Løvstad 1984, Cronberg et al. 1988, Hongve et al. 1988, Lepistö et al. 1994, Maileht et al. 2013). When present, this species most often dominates the phytoplankton community, creating mass occurrences and suppressing other species. Therefore, the focus here is mainly phytoplankton communities where there is no *G. semen* presence or dominance.

In addition to being inhabitants of already humic and dark colored lakes, the biomass of cryptophytes and chrysophytes are found to increase with increasing lake levels of DOC and browning (Arvola et al. 1996, Klug and Cottingham 2001, Weyhenmeyer et al. 2004, Urrutia-Cordero et al. 2017, Kankaala et al. 2019). However, a large-scale survey of Finnish lakes found that chrysophytes were actually less abundant in brown water lakes, and their abundance decreased with browning ((Taipale et al. 2016) and references therein). This indicates that even though chrysophytes are often present, and occasionally dominating humic lakes, they might be more abundant in clear lakes. The increases in certain species with increasing DOC and browning, often lead to decreases, or temporary absence of other species or taxonomic groups (Urrutia-Cordero et al. 2017, Kankaala et al. 2019).

Useful traits

Common traits among dominant taxa in humic and dark water lakes are motility, or slow sinking rates, and the ability to tolerate low light levels and low pH, as well as being competitive in stratified lakes with steep gradients of temperature, light and nutrients. Motility is mainly ensured by flagellae, which allow the algal cells to adjust their location in the water column. Most importantly, the algae can adjust towards better light availability, towards the surface. In stratified lakes, epilimnions are often and more rapidly depleted of especially P, but also N (Salonen et al. 1984). An additional benefit from vertical migration in these lakes is therefore the gained access to the more nutrient-rich hypolimnion. However, the ability to move between these layers, depends on the amplitude of migration, which again depends on cell size (Sommer 1988). Larger cells are able to migrate further during the hours of darkness, and are therefore more competitive in these conditions compared to smaller phytoplankton species (Sommer 1988, Drakare et al. 2003, Peltomaa and Ojala 2010). Motility is also possible without flagella, as in cyanobacteria, whom can adjust their location in the water layers by buoyancy according to light availability (Wetzel 2001).

Since the colors of irradiance that dominate the photic zone of lakes vary between lakes of different DOC concentrations and color, the pigment composition of phytoplankton may determine their abundance in humic lakes (Jones 1998). Depending on the content of chlorophylls in addition to chlorophyll-*a*, and particularly the content of accessory pigments and photoprotective compounds, algae species will be able to absorb different wavelengths of light (Figure 4) (Kirk 1983). Pigments which absorb wavelengths towards the green and red part of the PAR spectrum, will be advantageous in lakes where DOC attenuates the blue and some green wavelengths. In order to compensate for reduced light availability, most algae species, however not diatoms, are able to produce more light harvesting pigments, including chlorophylls (Wetzel 2001, Reynolds 2006, Faithfull et al. 2015). In one or two cell generations, chlorophyll content may be increased by 50 % on average (Reynolds 2006), giving the algae greater utilization of the available light. The productivity and carbon fixation rates will be equal as with lower chlorophyll-*a* content, only the algae will be able to perform at lower light intensities (Reynolds 2006). In addition to increasing light harvesting pigments, some algae species are also able to increase their concentrations of accessory photosynthetic pigments, widening the wavebands of absorbance, as illustrated in Figure 4 (Reynolds 2006). Especially cyanobacteria and cryptophytes (phycocyanins and phycoerythrins), chrysophytes and diatoms (xanthophylls) contain pigments that widen the absorption range between the peaks of chlorophyll-*a* (Figure 4) (Reynolds 2006). A combination of these traits, namely motility and adjustable pigment composition, will, mainly driven by lake color, determine the vertical presence of the specific taxa in the water column of stratified lakes (Longhi and Beisner 2009).

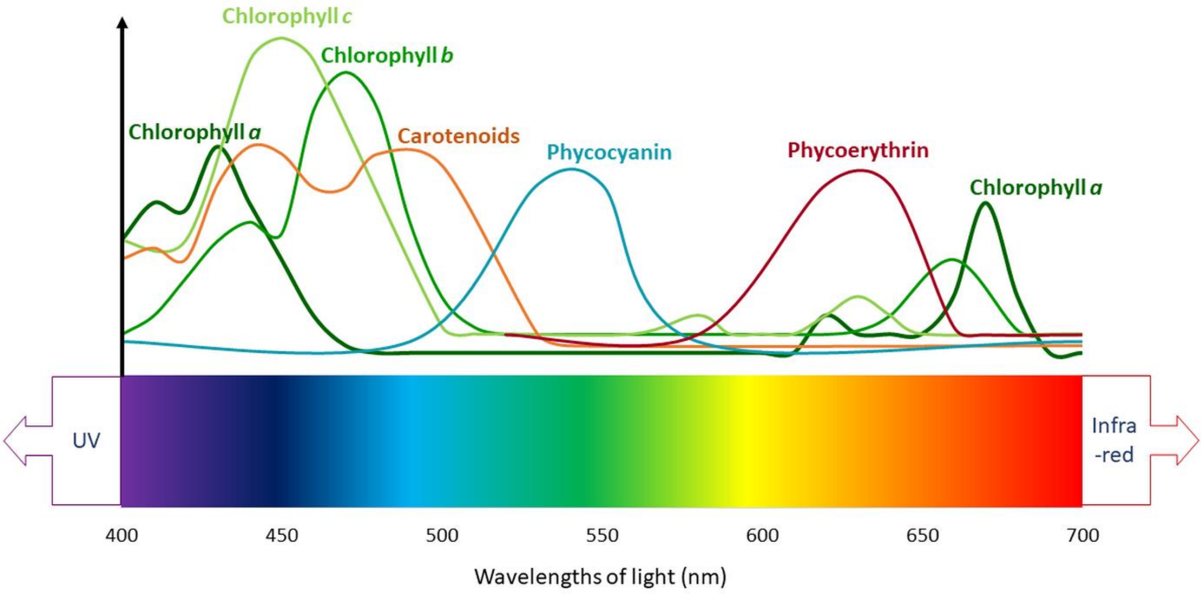

Figure 4. Absorption range of different algae pigments, including chlorophyll a, b, c, carotenoids and phycobilipigments (Roy et al. 2011), in the photosynthetic active radiation (PAR) spectrum of visible light.

In low light conditions, the capability to utilize the wavelengths and light available is crucial for growth and survival. In addition to pigment composition, and the ability to increase the chlorophyll *a* content of the cells, size and shape is important for maximized absorption of light energy. According to Kirk (1977), large, elongated cells are of great advantage in low light conditions, as they absorb plenty more light than for instance sphere-shaped cells.

In DOC rich conditions, where bacterial biomass increase and irradiance is reduced, mixotrophy is also a favorable trait, and species with this ability may increase their bacterivory in humic conditions (Wilken et al. 2018). Several of the known mixotrophic planktonic microalgae are common inhabitants of humic lakes, as mentioned above, mainly belonging to Cryptophyta, Chrysophyceae, Dinophyta and Chlorophyta (Olrik 1998).

Cryptohytes

Cryptophyta is a group of flagellated, unicellular algae, found in marine and freshwaters world-wide. They occur in a wide range of trophic states and during all seasons (reference in (Wetzel 2001, Reynolds 2006). Some species are colorless, and heterotrophic, however most are autotrophic.

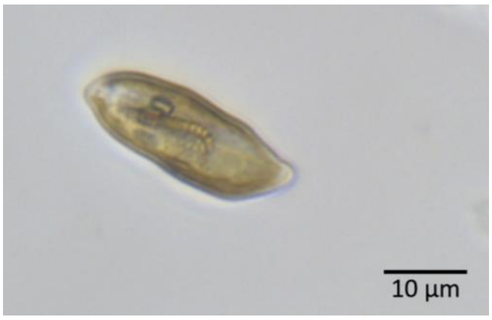

Figure 5. Cryptomonas *spp.*
Photo: Birger Skjelbred, NIVA

Pigmented cryptophytes contain chlorophyll *a*, chlorophyll *c2*, several xanthophylls (alloxanthin, crocoxanthin, monadoxanthin, zeaxanthin), α- and β-carotene, and one phycobilipigment (phycocyanin or phycoerythrin) which depends on the species (Chapman 1966, Schagerl and Donabaum 2003, Reynolds 2006). This combination of pigments allows cryptophytes to absorb wavelengths within the entire spectrum of visible light between the peaks of chlorophyll *a* at 430-660 nm, as seen in Figure 4. Hence, they are well adapted to low light, and are able to grow and reproduce in such conditions (Wetzel 2001). Due to their different pigment compositions, cryptophyte species appear either green or brown, as shown in Figure 5, and even red or blue (Wetzel 2001, Reynolds 2006). The competitive advantage of cryptophytes compared to brown (dinoflagellates, diatoms and chrysophytes) and green microalgae, is therefore, not surprisingly, found to be in the green part of the light spectrum ((Klaveness 1989) and references therein). Similar advantages are found for cyanobacteria (*Synechococcus* sp.) containing phycoerythrin (Klaveness 1989).

Cryptophytes are found to have biomass maxima in deep layers of the water column, often in metalimnion, with a large homogeneity of their occurrence (Reynolds 2006, Longhi and Beisner 2009). Mass occurrences of certain species are also found on the bottom of lakes (reference in Klaveness (1989)). The main genera of cryptophytes in humic lakes, *Cryptomonas*, are in addition able to perform diurnal vertical migration, where they reside in epilimnion or metalimnion during daytime, and migrate down towards hypolimnion in the early evening (Salonen et al. 1984, deNoyelles et al. 2016). The migration from hypolimnion onsets right before sunrise, before any solar radiation penetrates to the hypolimnion, indicating that this migrating behavior is driven by a circadian clock (deNoyelles et al. 2016). *Cryptomonas* therefore obtain optimal light conditions during daytime, performing photosynthesis, while also accessing hypolimnetic nutrients (P) during the night (Salonen et al. 1984). As hypolimnetic nutrient concentrations often are higher than the epilimnetic, where there is greater competition for the available nutrients, this DVM is a great competitive advantage for *Cryptomonas* spp. in stratified lakes.

Chrysophytes

Chrysophyceae (golden algae) are a diverse group of algae; unicellular, colonial or filamentous, flagellated or non-motile (Reynolds 2006). This groups is found on every continent (Nicholls and Wujek 2015), and they are well adapted to low temperatures ((Wetzel 2001) and references therein). Most chrysophytes are freshwater species, and they are mainly planktonic, however a few live attached to substrates (Nicholls and Wujek 2015). Members of this group range from strict photoautotrophic to strict phagotrophic (Olrik 1998). Chrysophytes are either scaled or naked, sometimes with loricas. Scaled genera (e.g. *Synura* or *Mallomonas*) are always autotrophic, while the naked (e.g. *Uroglena* and *Uroglenopsis*) or loricated (*Dinobryon*) can be mixotrophic (Olrik 1998). The extent of phagotrophy in mixotrophic chrysophytes seem to be dependent on light availability (Bird and Kalff 1989). An example of a loricated chrysophyceae is shown in Figure 6.

Figure 6. Dinobryon divergens.
Photo: Birger Skjelbred, NIVA

Chrysophytes are well adapted to low light levels ((Wetzel 2001) and references therein), and contain chlorophyll *c1* or *c2* in addition to *a* (Reynolds 2006). Their major xanthophyll is fucoxanthin (Reynolds 2006), giving them a golden-brown color, hence their alias golden algae. In addition, they also contain β-carotene and several other xanthophylls, for instance diatoxanthin and diadinoxanthin (Lewin and Guillard 1963), violaxanthin, antheraxanthin and zeaxanthin (Roy et al. 2011).

Chrysophyceae occur in a wide range of habitats, yet the largest abundance of chrysophytes are in low nutrient lakes, oligo- or mesotrophic, with low to moderate productivity (Wetzel 2001, Holopainen et al. 2003, Reynolds 2006, Taipale et al. 2016) ()(Nicholls and Wujek 2015). Chrysophyceae are reported as common both in highly colored, humic waters, and in clear waters (Olrik 1998, Holopainen et al. 2003, Nicholls and Wujek 2015). Similarly are nutrient demands of chrysophyceae variable and species-specific. They are good competitors for nutrients at low levels, especially for P (Nicholls and Wujek 2015). This is true for several species of *Dinobryon* and

Uroglena/*Uroglenopsis*, which may develop significant biomasses in low-P conditions (Wetzel 2001), however other species of *Dinobryon* and *Synura* in fact require high amounts of P (Wetzel 2001).

These differences are explained by the fact that various species respond differently to changes in DOC and light availability, in addition to species-specific nutrient demands and -lifestyles (Nygaard 1996, Wetzel 2001, Rottberger et al. 2013). Some species also have large adaptabilities for lake conditions (Nygaard 1996). For instance, the mixotrophic genera *Uroglena*/*Uroglenopsis* respond positively to increases in humic matter (Arvola et al. 1996), however it is found in both oligotrophic and eutrophic lakes (Nygaard 1996). *Uroglena*/*Uroglenopsis* is able to perform diurnal vertical migration (reference in (Nygaard 1996)), which may be of great advantage in humic conditions. Chrysophytes are mainly found to accumulate in deep layers of both humic and clear lakes (Nygaard 1996, Longhi and Beisner 2009), especially mixotrophs are reported as to be abundant in the metalimnion (Bird and Kalff 1989). However, *Dinobryon* species are found both at surface but also accumulating in deeper layers, up to 20 m depth, indicating that different species have different light demands (Nygaard 1996).

Members of the genera *Synura* and *Uroglena*/*Uroglenopsis* are occasionally causing blooms which results in bad taste and odor of the water, discoloring and which also have been linked to fish deaths (Løvik and Rognerud 1998, Hyatt et al. 2010). Such blooms of *Uroglena*/*Uroglenopsis* are also reported from Norwegian drinking water reservoirs, causing foul odor, however this occurred in a low nutrient, clear lake (Løvik and Rognerud 1998). In such low nutrient lakes, mixotrophy is of great advantage, hence this may also be a suitable environment for *Uroglena*/*Uroglenopsis*.

Diatoms

Algae of the class Bacillariophyceae – diatoms – are unicellular or colony-forming microalgae which all are surrounded by a characteristic silica shell. Diatoms are present in a range of habitats world-wide. Freshwater diatoms are mainly living attached to substrates and thus are mostly found in running water or the littoral zone of lakes, however several species also live freely as lake phytoplankton. Some species are able to grow heterotrophically when light is not available (Lewin and Guillard 1963), although diatoms are mainly autotrophic. Due to their silica exoskeleton, diatoms are dependent on $Si(OH)_4$ for optimal growth and reproduction, hence they may be more quickly limited by silicate deficiency than nutrients (N and P).

Diatoms are divided into two subgroups based on their shape and form; pennate and centric diatoms. Centric species are usually planktonic, and are generally non-motile (Cohn 2001). An example of a common planktonic, pennate diatom is shown in Figure 7. Motile diatoms are usually dependent on attachment to a substrate in order to perform a gliding movement, hence these are mainly adherent species (Cohn 2001). Planktonic species are surrendered to turbulence and mixing of the water in order to maintain their position in the photic zone (Wetzel 2001). However they tend to sink, especially in calm waters, and sinking rate depends on the species morphology and size (Wetzel 2001). In relatively calm waters, diatoms are therefore likely to have biomass peaks near the metalimnion, and are often found in deeper layers just as chrysophytes and dinoflagellates (Longhi and Beisner 2009).

Figure 7. A colony of the pennate diatom Diatoma vulgaris. *Photo: Birger Skjelbred, NIVA*

Diatoms contain, like chrysophytes, chlorophyll *a*, *c1*, *c2* and/or *c3*, β- and ε-carotene, fucoxanthin as main xanthophyll, in addition to diatoxanthin and diadinoxanthin (Lewin and Guillard 1963, Roy et al. 2011). Other xanthophylls may also occur, for instance violaxanthin, antheraxanthin and zeaxanthin (Roy et al. 2011). Diatoms adapt to low light intensities by changing their light-saturated photosynthetic rate, and reportedly do not increase their chlorophyll *a* content similar to other algae groups (Wetzel 2001).

Some species have a wide range of tolerances for environmental stressors such as low light, pH, heavy metals, pesticides or low nutrients (reference in (Gottschalk and Kahlert 2012)). Community composition in diatoms are greatly determined by water color and alkalinity (Fallu et al. 2002), and these communities respond quickly to stressors (Gottschalk and Kahlert 2012). Other responses may be changes in diversity or malformation of valves (Gottschalk and Kahlert 2012). For that reason, diatoms are often used as bioindicators for water quality, especially for pH and acidification, but also for impact of, for instance, DOC or water color, and for reconstruction of these conditions in paleolimnological studies (Fallu et al. 2002, Gottschalk and Kahlert 2012).

Dinoflagellates

Dinophyta is one of the most diverse groups of microalgae in terms of form and nutrition (Hackett et al. 2004). Most dinoflagellates are marine, only a little more than 10 % are freshwater (Burkholder et al. 2006). Some species produce toxins, and such toxic blooms can occur in marine waters (Hackett et al. 2004), however not in freshwater. Dinoflagellates are unicellular, and approximately 50 % of the known, free-living species are exclusively heterotrophic, while some are also mixotrophic ((Hackett et al. 2004, Burkholder et al. 2006) and references therein, (Olrik 1998)). Dinoflagellate cells are either naked or armored with a cell wall strengthened with cellulose or other polysaccharides (Hackett et al. 2004). Some species, usually armored, can be macroscopic, but this group ranges from > 100 µm to < 10 µm in size. Figure 8 shows a common planktonic, small, armored dinoflagellate.

Most photosynthetic dinoflagellates are quite similar to chrysophyceae and diatoms in pigment composition. They have chlorophyll *a* and *c*, either fucoxanthin or peridinin as main accessory pigment (Hackett et al. 2004, Reynolds 2006), in addition to β-carotene and other xanthophylls such as dinoxanthin and diadinoxanthin (Hackett et al. 2004). Hence, dinoflagellates are also golden-brown.

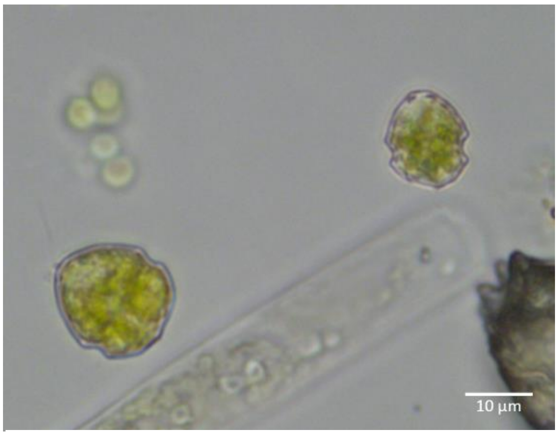

Figure 8. Parvodinium umbonatum. *Photo: Birger Skjelbred, NIVA*

Dinoflagellates as a group display a wide nutritional and morphological diversity and are adapted to a wide range of environments (Holopainen et al. 2003, Hackett et al. 2004). However, while some species are seemingly tolerant of a wide range of chemical conditions and are quite ubiquitous, most species are very restricted. Many species especially have narrow ranges of temperature and DOC, which seem to be the main controlling factors for their distribution (Wetzel 2001, Holopainen et al. 2003). Dinoflagellate species are also found to be restricted in terms of pH and calcium tolerance, however as a group, they are often common in slightly acidic lakes with low nutrient content (reference in Holopainen et al. (2003)). There are also size differences in dinoflagellate habitats in Swedish lakes, where large dinophytes (e.g. *Ceratium*) were found to be more common in eutrophic lakes, while small-sized species were more abundant in oligo-mesotrophic or dystrophic lakes (Willén 2003).

Some photosynthetic species have migratory behavior (Hackett et al. 2004, Burkholder et al. 2006). This behavior is driven by geotaxis (gravity), phototaxis (circadian rhythm, diurnal migration) and chemotaxis (chemosensory behavior) (Hackett et al. 2004, Burkholder et al. 2006). Usually, they move towards shallower depths during the day, towards their preferred light intensity where they reside (Hackett et al. 2004, Burkholder et al. 2006). Some species, due to their large size, are able to move over great distances in the water column (Sommer 1988, Hackett et al. 2004). Driven by phototaxis towards the end of the day, or chemotaxis related to predators or nutrient availability, and of geotaxis, the algae move deeper into the hypolimnetic zone during the night, where they find shelter for predators as well as increased access to nutrients (Hackett et al. 2004, Burkholder et al. 2006).

Other taxa

Chlorophyta and Charophyta (green algae) has the most diversity of habitats of the eukaryotic algae, although they are most represented in freshwaters, and range from microalgae to macroalgae (seaweeds) (Andersen 1992, Wetzel 2001). The microalgae can be both flagellated and coccoid, unicellular, colonies or filamentous. An example of a common planktonic, colony-forming species is shown in Figure 9. The group known by the common name desmids (Charophyta), are most common in unproductive, soft water lakes, and in waters with high DOC concentrations (Wetzel 2001).

Green algae are diverse in pigment content, and more similar to higher plants than other groups of microalgae. They all possess chlorophyll *a*, *b*, xanthophylls zeaxanthin, lutein, neoxanthin and violaxanthin, and many have β-carotene (Leavitt and Hodgson 2001, Wetzel 2001). The cells therefore mainly absorb blue and red light and are expected to be present in water layers where these wavelengths are available. They are often found higher towards the surface, in high irradiances, compared to e.g. cryptophytes, chrysophytes and diatoms, while they are also more vertically spread in the water column (Nygaard 1996, Longhi and Beisner 2009).

Figure 9. Ankistrodesmus fusiformis
Photo: Birger Skjelbred, NIVA

Cyanobacteria

Cyanobacteria are prokaryotic algae that can be unicellular, filamentous or in colonies. One example of a common, planktonic, colony-forming cyanobacteria is shown in Figure 10. They live in a wide range of habitats world-wide. They are photoautotrophs, and some species possess the ability to fix nitrogen (N_2) (Wetzel 2001).

Figure 10. Aphanizomenon klebahnii
Photo: Birger Skjelbred, NIVA

Cyanobacteria contain chlorophyll *a*, and accessory pigments phycocyanin and/or phycoerythrin (Reynolds 2006). Their pigment composition makes them capable of absorption of a wide range of wavelengths in the PAR spectrum (Figure 4), however some studies indicate that they are unable to utilize red light in humic lakes (Eloranta 1999 in (Steinberg et al. 2006)). Some species are shade-adapted, while others tolerate high light levels closer to the surface, depending on their pigment composition. Cyanobacteria are not flagellated, however some species are buoyant, adjusting their presence in stratified water columns with gas vesicles, in a limited vertical migration (Wetzel 2001). They can therefore position themselves across light and nutrient gradients (Wetzel 2001). In some instances, cyanobacteria are possibly driven by a circadian rhythm, suggested to determine the movement and position of the cells in the water column, as well as regulating their photosynthesis and nitrogen fixation (Wetzel (2001) and references therein)).

Experiments with humic substances (HS) showed that cyanobacteria was more limited (growth and photosynthetic activity) than a coccoid green algae to addition of HS, even at very low concentrations (< 0.3 mg L^{-1} DOC) (Steinberg et al. 2006). Several studies have also shown potential intracellular damage by humic acids or their photodegradation products on cyanobacteria (Steinberg et al. (2006) and references therein). This might be an explanation for the lack of cyanobacteria in humic lakes (Steinberg et al. (2006) and references therein).

The lack of domination or even absence of cyanobacteria in Nordic, humic lakes, could be due to the low nutrient content of northern lakes (Maileht et al. 2013), however a monitoring survey of humic and eutrophicated Norwegian lakes showed that one of the lakes had larger Secchi depth (> 3 m) and less nutrients (N, P) compared to the other lakes, and also lower chlorophyll *a*, and was more dominated by cyanobacteria, which were absent from the other humic lakes (Haande et al. 2012). This indicates that light availability, in addition to area and depth of the lake is important with regards to cyanobacteria.

Conclusions

Increasing humic conditions, when DOC concentrations exceed 10 mg C L^{-1} are likely to reduce primary productivity in Nordic lakes, which is limited by light attenuation. In addition, heterotrophic activity may increase, and lakes become net heterotrophic, depending on the phytoplankton species present, and benthic primary production.

As this review indicates, certain phytoplankton taxa occur regularly in humic lakes, regardless of the nutrient status and properties of the lake and catchment. However, on a species level, the communities are not overall the same. Common for the species inhabiting humic lakes, are the useful traits of being motile, preferably with diurnal vertical migration, having a pigment composition adapted to low light conditions and altered light quality, and some species also benefits from being mixotrophic. As diversity and biomass in humic lakes > 10 mg C L^{-1} seem to be limited by reduced light availability, the taxa dominating these lakes may just as well be the most tolerant species that are left behind when other algae are limited, and not necessarily species for whom these conditions are the most optimal.

Freshwater harmful algae blooms in Nordic countries are usually limited to cyanobacteria, with some incidents of chrysophytes causing bad smell and odor (Løvik and Rognerud 1998). The predicted continued browning of boreal lakes does not seem to favor cyanobacteria in Nordic lakes, however this might be dependent on the nutrient status of the lakes. Eutrophicated, humic lakes may have cyanobacteria blooms (Skarbøvik et al. 2019), however they might be outcompeted when light limitation or DOC concentrations becomes too high (Steinberg et al. 2006). From the literature assembled in this review, humic lakes do not appear to be under pressure from single species dominating the phytoplankton community and causing troubling mass occurrences, as long as the Raphidophyte *Gonyostomum semen* is absent or at least in low numbers. Together, the reports from humic, Nordic lakes, show that these lakes overall have a low low diversity, and periodic blooms of several of the presented algae groups may occur throughout the year (Rask et al. 1986, Haande et al. 2012).

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Figure 11. Lake Vansjø. Photo: Camilla H. Corneliussen Hagman