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Fish community responses to water colour – Results along a large gradient from clear to brown lakes in Sweden

Fisksamhällens respons på vattenfärg – Resultat längs en stor gradient från klara till bruna sjöar i Sverige

Stephanie Christine Koch

Master's thesis (självständigt arbete) • 30 credits
EnvEuro Environmental Science - Soil, Water and Biodiversity
Uppsala 2019

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Credits:	30 credits
Level:	Second cycle, A2E
Course title:	Master thesis in Environmental science
Course code:	EX0897
Programme/education:	EnvEuro Environmental Science - Soil, Water and Biodiversity
Course coordinating department:	Department of Aquatic Resources
Place of publication:	Uppsala
Year of publication:	2019
Cover picture:	Stephanie Koch
Online publication:	https://stud.epsilon.slu.se
Keywords:	water browning, climate change, dissolved organic carbon, fish community, community composition, fish biomass

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Abstract

An increase of dissolved organic carbon and iron in freshwater bodies across the Northern Hemisphere caused by environmental and land use changes lead to water browning with negative impacts on lake ecosystems. Effects of browning on aquatic ecosystems are complex and include reduced light penetration, thermal stratification, lower macrophyte cover, lower primary productivity, and potential shifts in species composition. However, little is known about impacts of browning on lake fish communities. In this study I analysed data from 146 lakes in Sweden along a large water colour gradient (measured as absorbance at 420 nm) to find out how fish community biomass is influenced by water colour. Furthermore, I studied if variations in species composition or mean body size contribute to differences in community fish biomass between clear and brown lakes. Therefore, I tested the relationship between absorbance and community biomass, species biomass, total abundance of fish individuals, mean fish body length, size diversity and species richness and the relationship between community composition and absorbance. The main result of my study was a negative relationship between fish community biomass and water colour, meaning a lower fish biomass in brown lakes than in clear lakes. The lower community biomass is likely explained by a lower biomass of several of the most common fish species, a lower total abundance of fish in dark lakes, and a lower number of species and differences in fish community composition. In contrast, I found no relationship between absorbance and fish body length, demonstrating that a lower biomass in brown lakes was not due to smaller fish. I also found that the variation in total fish abundance and biomass was high for clear lakes, but low for dark lakes. Also, values for highest biomass, highest number of individuals and number of species were much lower in darker lakes than in clear ones, explaining the lower community biomass with increased absorbance. Based on my results and considering that resource use and production are lower in dark lakes, I suggest a limitation of fish community biomass in brown lakes due to low resource availability. My study provides novel insights into fish community responses to absorbance, but also identifies further research needed in face of ongoing climate change and anticipated further water browning.

Keywords: water browning, climate change, dissolved organic carbon, fish community, community composition, fish biomass

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1 Introduction

Global climate change has huge impacts on the earth's ecosystems, and water bodies are especially affected (Woodward et al. 2010; Okorafor 2014). Climate change imposes multiple stressors on aquatic systems, like changes in temperature and precipitation, but also an increase in the magnitude and frequency of extreme weather events (IPCC 2014; Wrona et al. 2006). Aquatic systems are also stressed by other anthropogenic impacts, such as pollution, drainage, (habitat) alterations of water bodies, fisheries, recreational activities, or agriculture (Woodward et al. 2010; Wrona et al. 2006). Moreover, many species living in these systems have limited abilities to migrate in reaction to these changes (Wrona et al. 2006; Woodward et al. 2010; Poff et al. 2002), which is why they are specially affected by such stressors. One major implication of ongoing climate change and anthropogenic activities like changes in land use is browning of waters, which is especially pronounced in northern latitude water bodies (Karlsson et al. 2009; Monteith et al. 2007; Kritzberg and Ekström 2012).

Browning (also referred to as brownification, e.g. Monteith et al. 2007; Kritzberg and Ekström 2012; Finstad et al. 2014; Creed et al. 2018), is the shift in the optical properties of water towards a brown colour (Creed et al. 2018). This process is caused by increased concentrations of terrestrially derived dissolved organic carbon (DOC) and iron (Fe) (Kritzberg and Ekström 2012; Björnerås et al. 2017; Weyhenmeyer et al. 2014) in the water. Both rising DOC and Fe concentrations can be attributed to land-use changes (e.g. expansion of forestry, Björnerås et al. 2017; Kritzberg 2017), increasing terrestrial productivity in northern regions, and prolonged vegetation growing seasons (Finstad et al. 2016; Xu et al. 2013). Coupled with more heavy rainfall events (IPCC 2014), these changes alter hydrological processes and consequently the transport of organic carbons from soils into water bodies (Jansson et al. 2000; Larsen et al. 2011; Creed et al. 2018), leading to browner rivers and lakes (Williamson et al. 2015). Another cause of browning is the recovery from anthropogenic acidification, as the solubility of organic matter increases with decreasing acid deposition (Monteith et al. 2007; Wit et al. 2007). Thus, the causes for browning are manifold.

Browning has complex and interacting effects on aquatic ecosystems (Solomon et al. 2015). Higher levels of DOC (and therefore browner waters) lead to changes in optical properties and reduced (UV) light penetration, thereby shifting the relative availability of different habitats due to alteration of thermal niche size, increasing anoxic hypolimnetic zones and less light reaching water bottoms (Magnuson and Destasio 2008; Karlsson et al. 2009; Stasko et al. 2012; Craig et al. 2017). Browning of lakes may also increase thermal stratification and surface water temperature (Pilla et al. 2018). As light absorption restricts the photosynthesis of benthic algae and benthic energy mobilization, benthic primary production is negatively related to browning (Ask et al. 2009; Seekell et al. 2018). Pelagic production, however, may profit from the nutrient subsidies from terrestrially derived organic matter, and depending on nutrient and organic carbon availability, pelagic ecosystem productivity may sometimes even increase in brown waters (Jansson 2003; Ask et al. 2009). According to Finstad et al. (2014) an initial DOC increase from low levels can affect fish population biomass positively due to the nutrient increases, but further increases in DOC lead to declining biomass production as the nutrient increase cannot compensate for the lack of light. Hence, a hump-shaped response curve, representing the trade-off of higher DOC levels, is suggested (Finstad et al. 2014). Consequently, the decrease in benthic primary production cannot be compensated by increased nutrient levels (Ask et al. 2009). All in all, the above mentioned physical, chemical and biological effects caused by browning lead to lower primary and secondary production in lakes and therefore to lower overall lake productivity (Jansson 2003; Karlsson et al. 2009).

It is understood that benthic habitats are key energy pathways for production and biomass of higher trophic levels (Seekell et al. 2018; Karlsson et al. 2009; Bartels et al. 2016). Consequently, decrease of algal primary production and coupled reduction of zoobenthic prey are considered a key mechanism behind lower fish biomass in brown lakes (Benoît et al. 2016; Karlsson et al. 2009). Limited benthic production may not only have a negative impact on fish feeding through a lower availability of benthic invertebrates, but also because of loss of macrophyte cover (Stasko et al. 2012; Solomon et al. 2015). On the other hand, the response in pelagic production to DOC is context-dependent, varying with DOC-to-nutrient load ratio (Kelly et al. 2018), and can be positive or negative (see Jansson 2003; Vasconcelos et al. 2016). Despite the accompanying increases in nutrients in lake water with increases in terrestrial organic carbon, studies showed that lake productivity can be more affected by poor light conditions than by nutrient availability (Ask et al. 2009; Karlsson et al. 2015). As benthic primary production is consequently more sensitive to variation in water colour than pelagic production (Ask et al. 2009; Seekell et al. 2018), fish possibly switch to feeding in the pelagic zone (Bartels et al. 2016).

Generally, there is accumulating evidence that fish resource use and production is lower in dark humic waters than in clear (Karlsson et al. 2009; Karlsson et al. 2015; Benoît et al. 2016; van Dorst et al. 2019). Despite that, research mainly deals with specific fish species, whereas to my knowledge no studies have focused on fish communities over a large range of lakes so far. However, fish species or individuals react differently to changing physical factors in darker waters, which might either result in adaptation or physiological stress. In addition to a decline in prey availability, deteriorating visual conditions in humic waters impact fish foraging (Bartels et al. 2016). It is known that some fish species, like pikeperch (*Sander* *lucioperca*) or roach (*Rutilus rutilus*), are better adapted to impaired light conditions than others (e.g. perch, *Perca fluviatilis*) (Ljunggren and Sandström 2007; Estlander et al. 2010). Theoretically, differences between species in the ability to forage in clear and dark water can lead to competitive advantages for some species and thus, to a change in relative abundance of different fish species in response to browning. Similarly, predator-prey interactions may shift in response to browning as foraging success of visual predators and prey behaviour can be affected by deteriorated visibility (Ranåker et al. 2012; Ranåker et al. 2014). For example, pike foraging behaviour showed a decreasing reaction distance due to reduced optical conditions (Ranåker et al. 2012). Due to the fact that piscivore predation is considered a structuring force on fish communities changing piscivore-prey interactions in response to visibility conditions play an important role for understanding community shifts (Ranåker et al. 2012; Ranåker et al. 2014). Besides, differences in diet and feeding strategy may also influence varying species responses to browning. On one hand, resource availability might be more limited for benthivorous than for planktivorous fish (Bartels et al. 2016), on the other hand decreased visibility appears to affect piscivorous feeding more negatively than benthic feeding (Estlander et al. 2010; Estlander et al. 2012; Jönsson et al. 2013). However, responses differ not only between the different species, but also within species, depending on their size. Specifically, decreasing early growth rates and length-specific growth of fishes were observed in brown lakes, affecting biomass productivity (Benoît et al. 2016; van Dorst et al. 2019). Consequently, browning of waters can affect fish communities by prey limitation and changes in habitat availability, competition, predator-prey interactions, species distributions, feeding strategies, and physiological stress of fishes (Stasko et al. 2012).

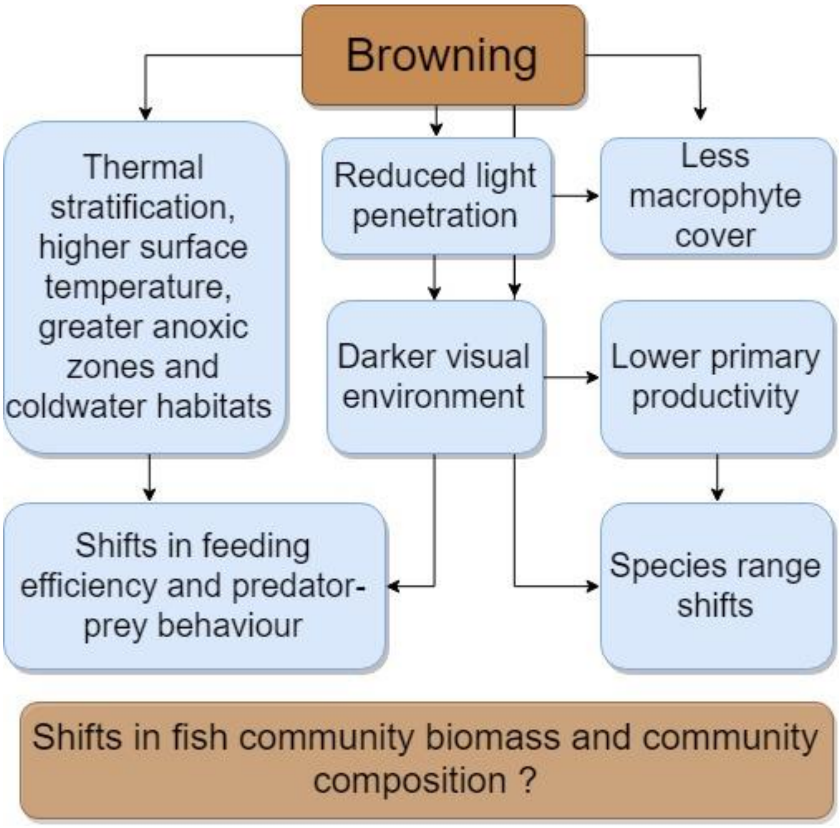

Figure 1: Potential effects of water browning on lake ecosystems and fish communities (adapted from Stasko et al. 2012).

Although shifts in fish communities in response to water browning are anticipated (Stasko et al. 2012; Ranåker et al. 2014), studies on actual community responses are to my knowledge not existent yet. Most research has focused on the response of single fish species (e.g. bluegill (*Lepomis macrochirus*): Craig et al. 2017; perch: Estlander et al. 2012; van Dorst et al. 2019; Bartels et al. 2016). Furthermore, many conclusions about responses to browning are based on small-scale experiments or data obtained at small spatial scales. Yet, Woodward et al. (2010) addressed the need of understanding biological responses to climate change at higher organizational levels (i.e. communities, food webs, ecosystems). In this regard, my study using a large data set on fish and environmental variables in the whole country of Sweden can be beneficial for understanding ecological responses at broad scales.

Here I ask to what degree water colour influences fish community biomass. Furthermore, I ask to what extent compositional variations or size structures within species contribute to differences in fish community biomass between clear and brown lakes. To study these community responses, I analysed data from 146 Swedish lakes across a large water colour gradient, ranging from clear to brown lakes. On one hand, my study can be seen as gradient study, showing and analysing observed fish community metrics and how existing variation in water colour can explain existing variation in fish community. On the other hand, it can be interpreted as space-for-time approach to get insights in how future climate change might affect lakes and fish communities. Whereas it can be a great benefit to use state-of-the-art observations for making predictions on further developments, the simplified approach of considering only one temporally changing environmental factor, namely browning, risks to leave out other potentially important environmental predictors.

2 Material and Methods

2.1 Lake selection

I conducted my analyses on a subset of lakes distributed across most of Sweden. These lakes were selected based on available surveillance data on sampling of fish and environmental variables for the years 2000 – 2015, rendering a total of 146 lakes. I extracted fish data from the Swedish national database NORS (National Register of Survey test-fishing - NORS 2019), which contains data from survey fishing conducted in many lakes in Sweden. Only lakes with fishing data from July or August were used for comparability and as these months are considered part of the main growing season for fish in this region and because environmental data is most often also available for these months. For comparability and avoiding any influence by different fishing methods, I filtered for fish survey data that was collected using specific benthic or pelagic gillnets (CEN, 2015). Furthermore, I decided to exclude lakes bigger than 500 ha from this study, as lakes with a small surface area (<500 ha) are considered more sensitive to environmental impacts (Stasko et al. 2012), and to ensure comparability between lakes. Other than that, I removed catch data of rainbow trout due to the fact that it is typically stocked for recreational fishing and cannot reproduce in Sweden. Additionally, there were a few cases of bream catches, where they could not identify the species (i.e. common bream (*Abramis brama*) or white bream (*Abramis bjoerkna*)) and therefore I removed these fish from my analysis. Similarly, I removed "carp fishes" from my analysis, as these represented undetermined cyprinids that could not be identified to species levels.

With the set of lakes extracted and filtered from the NORS database, I then checked for availability of environmental data in the Environmental database Miljödata MVM (Miljödata - MVM 2019). Lake chemistry information was included given a minimum of 5 years of data samples for the time period 2000-2015. As a measure of brownness of the water I used filtered absorbance at 420 nm. I also extracted information on surface area, mean lake depth, total phosphorus and water temperature. Only samples taken at a depth of 0.5 m were considered, to ensure comparability between lakes. For some lakes, the abiotic samples had been taken at the outflow of the lake, and in these cases, I removed them from the data set. After applying all these selection criteria, I ended up with a study data set of 146 Swedish lakes (Fig.2, Table A3).

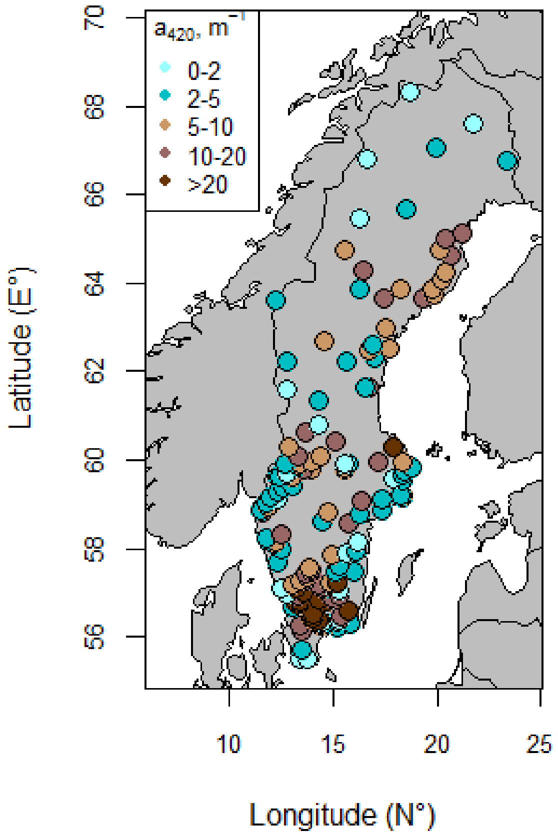

Figure 2: Location and absorbance of lakes. Data are shown for the 146 lakes analysed in this study. Low absorbance values are in blue and high absorbance values are in brown. Dark brown dots represent lakes with absorbance values ranging from 20 to 66 $a_{420}m^{-1}$.

2.2 Lake fish and abiotic data

The lakes in my dataset were located across the whole country of Sweden, and their surface areas ranged from 4 to 490 ha. Some lakes had test-fishing data from just one year, whereas others have been fished every year from 2000 – 2015. For lakes with multiple years of test fishing, mean data over the years was taken as basis for calculations and analyses. Measures used for my analyses are absorbance at 420 nm, lake area, type of fish net and number of nets used per lake, fish species, number of fish, length of individual fish, and weight per species per net. According to a standardized test-fishing method (Appelberg et al. 1995), the number of benthic gillnets used per lake depend on lake size and maximum depth, and the number of pelagic gillnets used on maximum lake depth (CEN). Benthic nets, with a net size of 45 m^2, were used in all 146 study lakes, whereas pelagic nets, with a net size of 82.5 m^2, were only used in 49 lakes as the other lakes were not considered deep enough for using them.

Absorbance measures the quantity of light that is absorbed by a sample (IUPAC, 1997). Absorbance at 420 nm (/5cm) is used as a measure of water colour (Kirk 1994) with high values indicating a brown colour. Low absorbance values of filtered lake water (0.45 m filter) were only given as <0.010, but in order to use the values for statistical analysis I set all these values to 0.009. In some cases, multiple data was available per year and in these cases I calculated the mean per year. Consequently, I calculated the mean values of all available absorbance measurements per lake for the time period 2000-2015. Thereafter, values were converted to the Napierian absorption coefficient a_{420} according to the recommendations of (Hu et al. 2002):

$$a_{420} = (AbsF_{420nm/5cm} * \ln(10))/OL \qquad (1)$$

where a420 is the Napierian coefficient, Abs420/5cm the measured absorbance of filtered water at 420 nm, and OL is the optical path-length (in m).

For simplicity, the Napierian coefficient is referred to as absorbance hereafter. For the 146 study lakes the absorbance varied between 0.5 and 66.6 m^{-1}, whereof 13 lakes had values above 20. As the focus of the study is on the direct effects of water colour in means of absorbance, I left out potential interactions with other environmental changes.

Altogether, 29 different fish species were caught and measured in the 146 study lakes (Table A1). In order to study the influence of the dominating fish species on community responses, the 5 most common species were selected for analysis, including perch, pike (*Esox lucius*), roach, ruffe (*Gymnocephalus cernuus*) and common bream. The most common species were determined via frequency of occurrence by calculating and ranking in how many of the 146 lakes each species appeared.

2.3 Data Analysis

To determine the impact of water colour on fish communities I studied the relationships between absorbance and catch per unit effort (CPUE, in gram or number of individuals per net area) for whole communities and the most common species, mean fish body length, species richness, and community composition. CPUE was used as a response variable as it is a common proxy for population biomass and abundance. Mean body length can be associated with resource use and limitation. Moreover, body size greatly affects the structure and functioning of aquatic communities and large ecological networks (Woodward et al. 2005). As lakes were sampled between 1 -16 years, I calculated the mean CPUE over the years. To calculate community $CPUE_{biomass}$ per lake I first combined the weight of all individuals of all species and then divided their total biomass by net area. Species-specific CPUE was calculated in the same way by summing up the weight of all fish caught of a species per lake and dividing it by net area. For $\text{CPUE}_{\text{numbers}}$ the summed number of individuals per lake in total was divided by net area.

For fish body length data, I calculated the mean total body length over all sampling years per species and for the whole fish community. In addition, I calculated skewness of length to see if the relative proportion of small to large individuals differs with absorbance.

Moreover, I calculated size diversity for each lake fish community using individual length measurements. Size diversity presents part of the functional diversity of a community as body size combines several traits that influence community functioning, and is therefore ecologically important (Woodward et al. 2005; Brucet et al. 2018). For the calculation I used the open source software 'diversity08' by Quintana et al. (2008) available at >www.limnolam.org>. Following this nonparametric method, the size diversity index (my) is computed using the Shannon diversity expression as basis and adapting it for continuous variables like size (Quintana et al. 2008). Size diversity is calculated as an integral including the probability density function (pdf; e.g. a function that describes the relative likelihood for a random variable to take on a given value) of the size of the individual fishes described as follows:

$$\mu = -\int_{0}^{+\infty} p_x\,(x) log_2 p_x(x) dx$$

where px(x) is the pdf of size x (Brucet et al. 2018; Quintana et al. 2008). Size diversity per lake community shows the size variation of all individuals of a lake and with the regression analysis I could see if size diversity is affected by brown water colour.

Another measure I included is species richness, which is also a proxy of biological diversity of lake fish communities. Species richness is defined as "the number of species of a given taxon in the chosen assemblage" (Magurran 2004). More specifically, I used total species density per lake community observed over years as measure for species richness. Therefore, I counted the number of observed species per lake over all fish sampling occasions.

Given that there are multiple factors that can influence size and diversity of fish, I decided to test if the potential influence of absorbance on response variables holds also when including lake area as a covariate. I chose to include lake area as a covariate for absorbance in all regression analysis, because area might especially limit fish biomass and diversity (Matuszek and Beggs 1988) and because data was available for all lakes. The relationship between lake area and absorbance resulted in a factor of -0.2550058.

I analysed the relationship between absorbance and CPUE, fish length, species richness and size diversity using regression models with lake area as a covariate. As I wanted to know the effects of absorbance on fish metrics, absorbance depicted the independent value and all fish specific measures were analysed as dependent variables. Linear regression models were used for all measures except community composition and for $CPUE_{biomass}$ and $CPUE_{numbers}$ I additionally applied quantile regression models for the quantile levels 0.10, 0.50 and 0.90 to get further insight. Fish metric data was ln-transformed for normalization prior to regression analyses. Also, I conducted a visual inspection of residuals of CPUE, length data, number of species and size diversity from linear regressions. Non-significant interaction terms for absorbance and lake area were removed before analysing the separate effects of absorbance and lake area on the respective response values. Apart from that, I focused on the direct effects of browning only and left potential interactions with other environmental changes out of my study.

To depict the variation of species composition in communities associated with differences in water colour, I carried out non-metric multidimensional scaling (NMDS). This was done using the *metaMDS* fuction in the package *vegan* in R (Oksanen et al. 2019). Stress levels were under 0.2 in all runs, which showed that the data was suitable for two-dimensional interpretation. For visualisation of differences between lakes with NMDS, I divided my lake data set into two equally big groups by determining the median absorbance value and labelling all lakes with values lower than the median (5.41) as clear and all lakes with higher absorbance values as brown lakes. With the input of lake identification number, fish species and species-specific biomass, a similarity matrix was generated. Based on this matrix of the multidimensional data a two-dimensional graph was computed. Subsequently, I tested for significant differences in fish community composition across clear and brown lakes with permutational multivariate analysis of variance (PERMANOVA). PERMANOVA was carried out with 999 permutations, using the *adonis* function in the *vegan* package. All statistical tests and plots were done in R 3.5.1 (R Core Team 2018).

3 Results

Linear regression analyses revealed the relation of community biomass, the biomass of several of the most common species, total fish abundance, community length, length for several of the most common fish species, size diversity and species richness to absorbance, and additionally the effect of lake area as covariate (Table 1). From additional quantile regression analyses for community biomass and total fish abundance I obtained more detailed information on community responses (Table A2). Lastly, NMDS and Permanova showed the differences between fish communities in clear and brown lakes (Fig.8).

Table 1: Statistical Results from the linear regression analysis

Response variable	F	R^2	Explanatory variable	Parameter (SE)	T	p
Community biomass (CPUE) (LN)	F(2, 143) = 5.303**	0.069	Intercept	3.200 (0.103)	31.069	< 2e-16 ***
			Absorbance	-0.019 (0.006)	-3.252	0.00143 **
			Area	-0.00037 (0.0005)	-0.639	0.524
Perch biomass (LN)	F(2,177) = 0.152	0.002	Intercept	2.007 (0.202)	9.906	< 2e-16 ***
			Absorbance	-0.004 (0.013)	-0.333	0.739
			Area	-0.001 (0.001)	-0.507	0.613
Pike biomass	F(3,115) = 3.636*	0.087	Intercept	1.023 (0.192)	5.319	5.2e-07 ***

Response variable	F	R^2	Explanatory variable	Parameter (SE)	T	p
(LN)			Absorbance	-0.023 (0.012)	-1.969	0.514 .
			Area	-0.005 (0.002)	-3.118	0.0023 **
			Absorbance*Area	0.0004 (0.0002)	1.724	0.0873 .
Roach biomass (LN)	F(2,101) = 4.149*	0.076	Intercept	1.986 (0.218)	9.11	8.19e-15 ***
			Absorbance	-0.036 (0.132)	-2.752	0.00703 **
			Area	-0.002 (0.001)	-1.492	0.139
Ruffe biomass (LN)	F(2,46) = 1.871	0.075	Intercept	-2.064 (0.396)	-5.209	4.34e-06 ***
			Absorbance	-0.011 (0.023)	-0.502	0.618
			Area	0.003 (0.002)	1.695	0.0968 .
Bream biomass (LN)	F(2,31) = 1.19	0.071	Intercept	0.742 (0.402)	1.846	0.0744 .
			Absorbance	-0.008 (0.018)	-0.474	0.639
			Area	0.002 (0.002)	1.194	0.242
Total fish abundance (CPUE) (LN)	F(2,143) = 8.447 ***	0.106	Intercept	-0.524 (0.128)	-4.103	6.83e-05 ***
			Absorbance	-0.029 (0.007)	-4.042	8.61e-05 ***
			Area	-0.0002 (0.0007)	-0.282	0.779
Community length (LN)	F(2,143) = 1.357	0.019	Intercept	4.914 (0.026)	189.208	<2e-16 ***

Response variable	F	R^2	Explanatory variable	Parameter (SE)	T	p
			Absorbance	0.002 (0.001)	1.344	0.181
			Area	-0.000 (0.000)	-0.589	0.557
Perch length (LN)	F(2,177) = 0.398	0.004	Intercept	4.866e+00 (3.056e-02)	159.238	<2e-16 ***
			Absorbance	1.602e-03 (1.932e-03)	0.829	0.408
			Area	-2.138e-05 (1.738e-04)	-0.123	0.902
Pike length (LN)	F(3,138) = 2.956 *	0.060	Intercept	6.251e+00 (4.036e-02)	154.894	<2e-16 ***
			Absorbance	-7.562e-03 (2.614e-03)	-2.893	0.00443 **
			Area	-7.288e-04 (3.391e-04)	-2.149	0.03336 *
			Absorbance *Area	1.084e-04 (5.161e-05)	2.100	0.03757 *
Roach length (LN)	F(2,134) = 0.488	0.007	Intercept	4.913e+00 (3.343e-02)	146.971	<2e-16 ***
			Absorbance	1.422e-03 (2.180e-03)	0.652	0.515
			Area	-9.952e-05	-0.571	0.569

Response variable	F	R^2	Explanatory variable	Parameter (SE)	T	p
				(1.742e-04)		
Ruffe length (LN)	F(2,52) = 4.903 *	0.159	Intercept	4.399 (0.042)	104.463	<2e-16 ***
			Absorbance	0.007 (0.003)	2.579	0.0128 *
			Area	-0.0002 (0.0002)	-1.140	0.2597
Bream length (LN)	F(2,40) = 0.482	0.024	Intercept	5.321 (0.092)	58.147	<2e-16 ***
			Absorbance	0.003 (0.004)	0.591	0.558
			Area	-0.0002 (0.0004)	-0.504	0.617
Size diversity (LN)	F(2,143) = 2.442 .	0.033	Intercept	0.664 (0.022)	29.626	<2e-16 ***
			Absorbance	0.003 (0.001)	2.099	0.0376 *
			Area	0.0001 (0.0001)	1.190	0.2359
Species richness (number of species) (LN)	F(2,143) = 19.89 ***	0.218	Intercept	3.847 (0.294)	13.077	<2e-16 ***
			Absorbance	-0.018 (0.017)	-1.063	0.29
			Area	0.01 (0.002)	5.76	4.95e-08 ***

. <0.1, *<0.05, **<0.01, ***<0.001

3.1 Community biomass

Lake community $\text{CPUE}_{\text{biomass}}$ was negatively related to absorbance (Figure 2, Table 1). This negative relationship was mainly caused by lower maximum biomass levels in brown lakes (Fig. 2b, Table A2). The variation in biomass is clearly higher between lakes with improved clarity (Fig. 2).

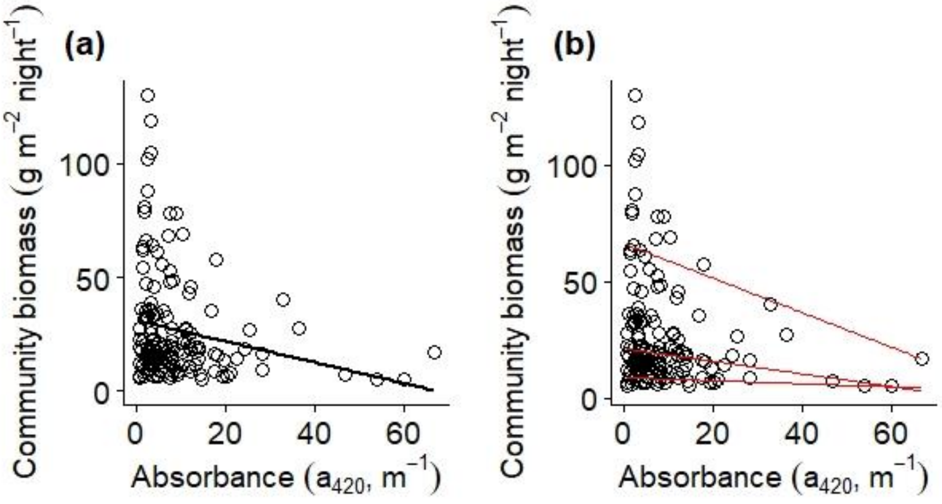

Figure 3: The relationship between community biomass and absorbance showing (a) a significant linear relationship ($p<0.05$) in black and (b) quantile regression lines in red, with the 0.5 and the 0.9, but not 0.1, quantile lines representing significant relationships. Each black circle represents observed data from an individual lake. It has to be noted that the regression lines in plots are only based on absorbance, whereas statistical analyses included lake area as co-variate.

3.2 Species specific biomass

There was a significant negative relationship between absorbance and pike and roach biomass (Fig. 4, Table 1). There was a negative trend, but not significant, between the biomass of the other three species analysed (perch, ruffe and bream, Fig. 4, Table 1). Also, for pike $\text{CPUE}_{\text{biomass}}$ there was a significant interaction between absorbance and lake area, suggesting that the relationship between absorbance and pike biomass differs depending on lake size (Table 1).

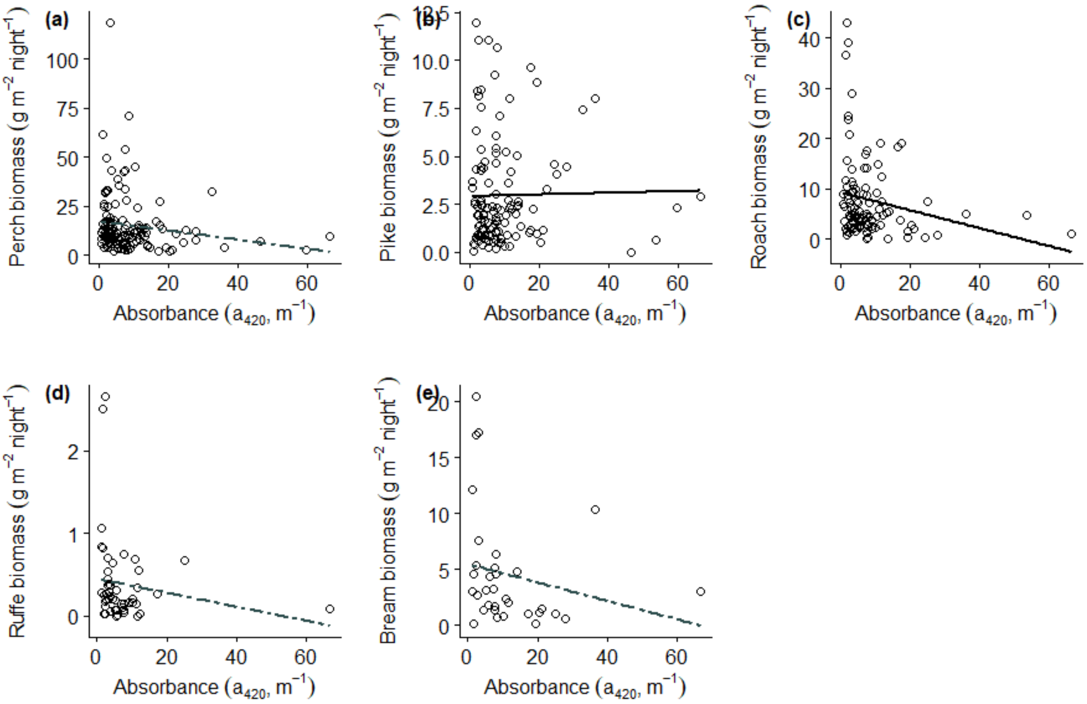

Figure 4: The relationship between biomass of a) perch, (b) pike, (c) roach, (d) ruffe, (d) bream and absorbance. Each black circle represents observed data from an individual lake. Solid regression lines represent significant ($p<0.05$) linear relationships, dashed lines non-significant linear relationships. It has to be noted that the regression lines in plots are only based on absorbance, whereas statistical analyses included lake area as covariate.

3.3 Community abundance

The total abundance of fish individuals ($\mathrm{CPUE}_{\mathrm{numbers}}$) was negatively related to absorbance (Figure 5, Table 1). Similar to $\mathrm{CPUE}_{\mathrm{biomass}}$, between-lake variation in $\mathrm{CPUE}_{\mathrm{numbers}}$ seems to be lower with darker water colour and the lower $\mathrm{CPUE}_{\mathrm{numbers}}$ was caused by maximum, rather than mean abundance of fish individuals (Table A2).

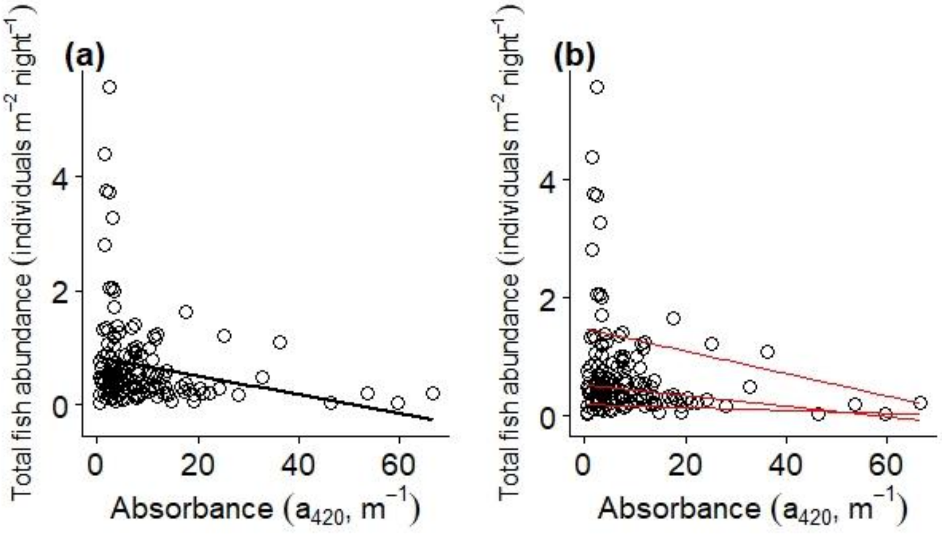

Figure 5: The relationship between total fish abundance and absorbance with the regression line representing a significant ($p<0.05$) linear relationship. Each black circle represents observed data from an individual lake. It has to be noted that the regression line in the plot is only based on absorbance, whereas statistical analyses include lake area as covariate.

3.4 Community mean length and length diversity

In contrast to community biomass, there was no relationship between mean fish body length in lake fish communities and absorbance (Figure 6, Table 1). However, I did find species-specific body size responses to absorbance, with ruffe having a positive, biologically significant relationship and pike having a slightly negative, biologically weak (but significant) relationship to absorbance. Just like for pike biomass, there was an interaction between absorbance and lake area on pike length, Absorbance did not affect skewness of fish body lengths ($p=0.848$, $F(1, 144) = 0.03684$)).

However, there was a positive relationship between length diversity and absorbance (Figure 6 (b), Table 1).

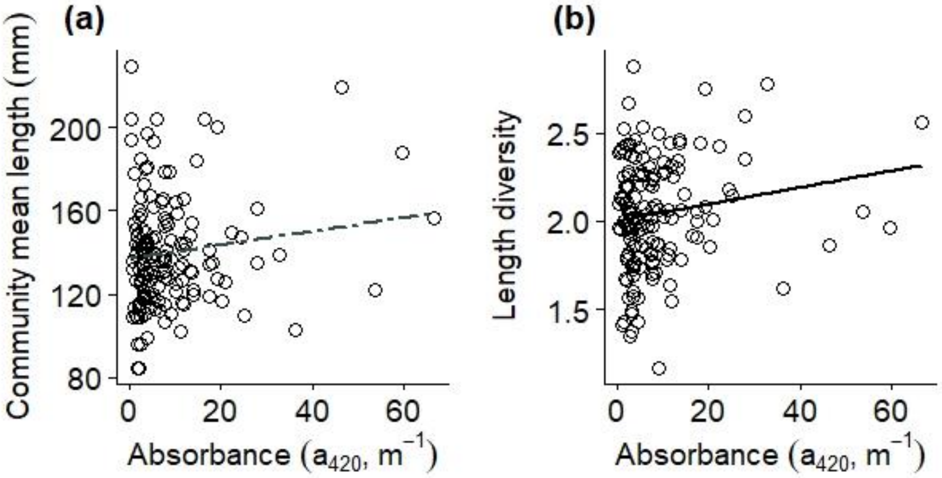

Figure 6: The relationship between absorbance and (a) mean individual fish length per lake fish community with a dashed line representing a non-significant linear relationship; (b) length diversity with the solid regression line representing a significant ($p<0.05$) relationship. Each black circle represents observed data from an individual lake. It has to be noted that the regression lines in plots are only based on absorbance, whereas statistical analyses included lake area as covariate.

3.5 Species richness and community composition

There was a non-significant negative relationship between species richness and absorbance (Figure 7, Table 1). Altogether, 29 species were caught in the study lakes, but some species just occurred in a few lakes or were only abundant in clear lakes. Community composition differed between clear and brown lakes (PERMANOVA, F=4.3514, p=0.001). However, most fish communities consisted of the same common species, but their occurrence was reduced in browner lakes, as results above imply. The NMDS analysis shows that the fish communities do not differ essentially in the occurring species depending on water colour, but that brown lake communities are composed of fewer species (Fig. 8).

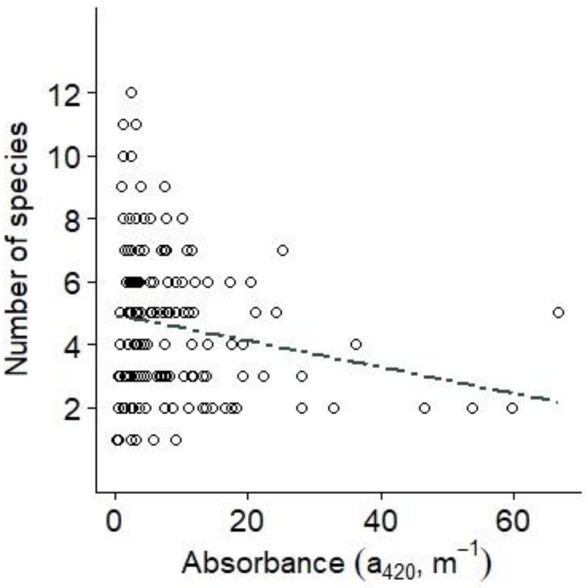

Figure 7: The relationship between absorbance and species richness with the dashed regression line representing a non-significant (p>0.05) relationship. Each black circle represents observed data from an individual lake. It has to be noted that the regression lines in plots are only based on absorbance, whereas statistical analyses included lake area as covariate.

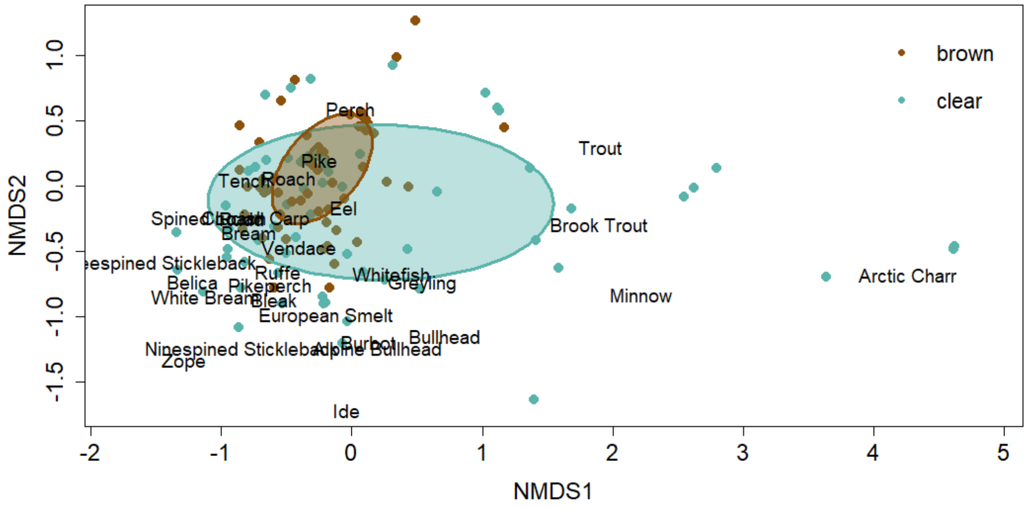

Figure 8: Two-dimensional non-metric multidimensional scaling plot showing the difference in community composition between clear and brown lakes. Clear lakes are indicated with blue dots and brown lakes are indicated with brown dots. Species far away from each other in the plot are less likely to occur in the same lake than species plotted close to each other. Mean community composition in clear lakes is depicted by the blue circle, and community composition in brown lakes is depicted by the brown circle.

4 Discussion

I found that a higher absorbance, thus a darker water colour, has a negative influence on fish community biomass. This was associated with lower biomass of the most common species, a lower number of fish individuals and differences in community composition in brown lakes. In contrast, I found no relationship between absorbance and mean fish body length. The low community biomass in dark lakes was not because of one specific species having a lower population biomass but was rather due to a lower biomass across many species, albeit only significantly for some. The difference between fish communities in clear and brown water lakes was mainly because communities in brown lakes appeared to be more homogeneous compared to clear water communities that were composed of more different species.

Several different processes and factors can cause the observed lower fish community biomass in brown compared to clear lakes. I found more variance in biomass in clear lakes than in brown lakes and determined that especially the maximum possible fish biomass is negatively impacted by dark water. This suggests that fish biomass is probably limited by low resource availability in dark lakes and that the maximum (rather than mean) fish community biomass is limited by dark water. Previous studies came to similar conclusions, as lower benthic primary production (Karlsson et al. 2009) and a subsequent decrease in zoobenthos biomass (Stasko et al. 2012) are likely to lead to lower (maximum) fish biomass (Solomon et al. 2015; Craig et al. 2017). Previous studies found that biomass production, but not standing stock biomass, was lower in dark lakes (e.g. Karlsson et al. 2015; van Dorst et al. 2019). Albeit I did not look at production, I found that standing stock biomass was indeed lower in dark lakes when looking at whole fish communities. The decline in community biomass was the result of a general biomass loss of many species (even though this was only statistically significant for a few species). Despite potential species-speciec adaptations to dark light conditions (turbid or dark water colour) might benefit some species, I mainly found no or negative responses. Previous studies suggest that environmental conditions in dark-coloured lakes are considered unfavourable for perch (Estlander et al. 2010), as they depend on good light conditions for visual predation (Helfman 1979) and prefer structural complex habitats with macrophytes (Diehl 1988). Despite that, perch $\mathrm{CPUE}_{\mathrm{biomass}}$ has already been reported in a previous study, and also here in my study, to show no relation to brown water colour (van Dorst et al. 2019). Roach, on the other hand, is better adapted to feeding at low light intensities (Bohl 1980) and foraging in simple structured habitats (Persson 1987), but despite these adaptations, roach was significantly negatively related to absorbance in my study. Therefore, there must have been other factors than visibility, like resource limitation for example, that lead to a lower roach biomass in brown waters. When pike foraging behaviour was tested in brown water, capture success was high (Jönsson et al. 2013) and there was no difference in strike distance compared to in clear water (Ranåker et al. 2012). Nonetheless, pike biomass was negatively (but weakly) related to dark water colour in my analysis. Benthic fish could be hypothesized to be more significantly affected by the impacts of reduced light penetration and lower benthic primary production. This does not seem to be the case in my study set, even though I did not test for it specifically. Still, the bottom dwelling, benthivorous species ruffe and bream (Ogle 1998; Löffler 1984) only showed a non-significant negative relationship to absorbance. Thus, different adaptations of fish species to darker water did probably not influence their responses. Instead, the likely low resource production in dark lakes might impact most fish species negatively. Nonetheless, more research is needed to resolve knowledge gaps.

Results demonstrated that the observed negative relationship between community biomass and absorbance is due to few fish rather than smaller fish. It has already been reported earlier that common fish species in Canada decrease in abundance with higher DOC concentrations (Benoît et al. 2016). Hedström et al. (2016) reported that brownification increases the winter mortality and decreases body condition and prey biomass ingestion in three-spined stickleback (*Gasterosteus aculeatus*) due to a decreased search efficiency when feeding in dark waters. Therefore, in addition to lower prey availability, a higher winter mortality of fish in brown lakes might be one reason for lower fish biomass in brown lakes. Differences in mean fish body size, in contrast, were not observed in relation to absorbance and did therefore not influence fish biomass levels. In the case of specific fish populations, like bluegill or perch, literature reported substantial differences in maximum size and size at age between dark and clear lakes (Craig et al. 2017; van Dorst et al. 2019), indicating a relation between absorbance and fish length. From these results, a trend towards lower mean fish length in relation to absorbance could have been assumed. Even though this was not the case, a lack of difference in mean length between lakes with different water colour does not mean that there is no growth response (see van Dorst et al. 2019). Also, fish length response at community level seems to differ from population level responses. This could be due to different species compositions in dark and clear lakes, as the mean fish body size of a community is a function of abundant species. In contrast to mean body size, I found that size diversity in communities was positively influenced by darker water colour. Given that community niche space is mainly determined by body size (Woodward et al. 2005), changes in size diversity may lead to shifts in community structure (García-Comas et al. 2016; Brucet et al. 2018). Regarding this, a high size diversity in dark lakes would suggest a diversified trophic niche use within communities. Nonetheless, it is unknown whether size diversity response is interrelated with the absorbance-biomass relationship.

Dark waters do not only constrain the number of fish individuals, but also fish community composition. Even though a relationship between absorbance and a loss in species richness could not be proven statistically, communities in clear lakes appeared to comprise more species than brown water lakes. Community composition differed noticeably between clear and brown lakes, with some species like arctic charr, minnow or burbot not being present at all in darker lakes. Perch, pike and roach were the most commonly occurring species in my lake data set, which is typical for small boreal forest lakes (Olin et al. 2010) and this did not differ with lake colour. A constrained species composition in darker lakes definitely impacted community biomass, considering that the species that occurred in brown lakes additionally showed lower biomass than in clear lakes. Further research is needed to understand differences in community composition with water colour, where potential factors could be shifts in dominance of certain feeding guilds or fish orders. Investigating all these before mentioned factors on the level of whole communities is a novelty and contributes to the current knowledge on effects of browning in temperate and boreal lakes, adding to earlier studies that have mainly focused on specific species and populations (Finstad et al. 2014; Benoît et al. 2016; Craig et al. 2017; van Dorst et al. 2019).

There are also other mechanisms that could influence community biomass and other community metrics, which were not addressed in my study. For example, the influence of variables such as water colour on community structure can be density dependent, e.g. through competition or predation (Olin et al. 2010; Horppila et al. 2010). Horppila et al. (2011) showed that darker water colour strongly affected fish feeding rate because of decreased visibility. A decreased search efficiency and a changing food selectivity in fishes due to darker water colour has also been found in other studies (Estlander et al. 2010; Estlander et al. 2012; Olin et al. 2010; Ranåker et al. 2014). Although these previous studies did not investigate population responses, it can be assumed that a reduced fish feeding rate probably impacts fish biomass. Thus, a reduced feeding rate in darker lakes might be one reason for a lower community biomass in my study. Furthermore, fish communities in darker lakes could be impacted by a lower food web efficiency. This might be the case because browning can favour microbial loops, which, in turn, lead to reduced energy levels at higher trophic levels, and thereby a lower fish biomass (Lefébure et al. 2013).

Moreover, abiotic factors also need to be considered when assessing impacts of water colour on lake fish communities. Thermocline depth, a proxy for habitat availability, for example, is reported to be negatively related to DOC concentrations (Craig et al. 2017). However, they found that fish CPUE was positively related to thermocline depth. This suggests that the well-oxygenated epilimnion decreases with higher absorbance and consequently fish biomass decreases. Furthermore, phosphorus, which is an indicator of lake productivity, could act as predictor for fish growth rate and abundance (Benoît et al. 2016). Additionally, pH values also influence fish biomass (Horppila et al. 2010) and can be a valid covariate in fish biomass analyses. A study by Seekell et al. (2018) suggested a moderating effect of lake morphometry on the relationship between water colour and fish biomass. Whereas I addressed this issue to some extent by including lake area as a covariate, they focused on the influence of mean lake depth, as the depth influences the degree of light extinction. All above mentioned factors are just a few examples of influencing factors on fishes that need to be further studied in the combination of fish communities and water colour.

It goes without saying that the effects of browning vary depending on the context and the initial state of the lake (Williamson et al. 2015). While I looked at differences between already clear and brown lakes (space-for-time approach) and not changes over time, investigating temporal shifts in lake fish communities would be another element worthwhile to look at, given the availability of data covering long enough time series. For example, it is hypothesized, that initially clear oligotrophic lakes are more sensitive to browning than lakes with higher initial dissolved organic matter loadings (Williamson et al. 2015). However, Finstad et al. (2014), found an initial increase in fish CPUE due to increasing DOC, followed by a subsequent decline with ongoing DOC increases. Therefore, they suggested a unimodal fish yield response due to water DOC, depending on starting values of DOC.

Although my study would suggest a decreased fish biomass in northern lakes that become increasingly brown, climate change impacts like warming and a subsequent productivity increase in the north might also lead to different reactions. Hayden et al. (2017) studied lakes in the subarctic and demonstrated that climate change leads to increased lake productivity and consequently to increased fish density and biomass, but also to a decreasing size among individuals of the community. Thus, I want to highlight the crucial factor of ecoregion and initial temperature of lakes when making predictions about biomass responses to climate change.

In view of my findings, I would argue that no single factor is responsible for the difference in community biomass along the water colour gradient, but that there are several contributing factors. It is suggested that the lower community biomass is linked to negative responses of several species rather than one or two dominant species. Moreover, the biomass loss is reinforced by a reduction in species abundance and individual fish abundance. With ongoing climate change, further browning in the future is anticipated (Larsen et al. 2011; Seekell et al. 2018; Weyhenmeyer et al. 2016; Seekell et al. 2015) and therefore more research and knowledge, but also adaptive management strategies are needed. A study modelling future scenarios for Swedish lakes considering climate change effects calculated worst-case absorbance increase factors between 1.1 and 7.6 (with a median of 1.3; Weyhenmeyer et al. 2016). Seekell et al. (2015) even estimated a loss of 8.7 % in whole-lake primary production per decade for southern Sweden due to DOC. Therefore, it is likely that fish biomass will decrease in many Swedish lakes, which could also impact biodiversity, food-web stability, ecosystem-function, food provision and economics. Nonetheless, the adaptive capacity of fishes may to some extent mitigate the intensity of such adverse effects. On the contrary, it has been indicated that fish populations in darker lakes might be less resilient to sustained fishing pressure (Craig et al. 2017). However, I would argue that it is important to incorporate lake browning effects on fish communities for sustainable fisheries management (see also Benoît et al. 2016).

5 Conclusion

In conclusion, a darker water colour showed to have a negative effect on fish community biomass. I studied different community metrics of a large data set with lakes ranging from clear to brown water colour and inferred, that not one factor leads to a lower biomass in brown lakes but rather that several influencing factors together lead to a biomass loss. As communities in browner lakes appear to compose fewer species and even the occurring species show a lower biomass and lower number of individuals, this might be the primary underlying reason for community biomass loss.

In face of ongoing climate change and further water browning being predicted, my study provides novel insights into effects of environmental and anthropogenic stressors on fish ecology. As this is probably the first study focusing on the response of fish communities to absorbance, further research is needed and suggested. In order to enhance understanding and make forecasts, possible shifts in community composition, changes over time and more community metrics need to be studied in relation to water colour. For example, reproduction success, growth or mortality could be possible measures to look at. Moreover, it could be investigated if certain feeding guilds or fish orders dominate in darker lakes and lead to compositional changes. Finally, as fish community biomass is adversely affected by water colour, this needs to be considered when managing lakes affected by browning.

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Acknowledgements

I would first like to thank my thesis supervisors Magnus Huss and Renee van Dorst for their great support, useful comments and full engagement throughout the thesis process. I am happy to have chosen to write my thesis at the Aqua institute. I would also like to thank for the opportunity to conduct fieldwork for the Aqua institute which was a great balance to the thesis work. A big thank you also to all my friends and study colleagues who gave advice, answered questions and listened to my thoughts or problems. Thanks also to my co-supervisor Stefan Schmutz. Finally, I must express my gratitude to my family for providing me with continuous support and encouragement throughout all the years.

Thank you.

Stephanie Koch

Popular summary

Climate change, including higher temperatures, more intense rainfall events and longer growing seasons, together with human activities, such as changes in land use, put pressure on aquatic systems. One example, that is especially evident in the northern parts of the earth, is the process of water browning. Water browning implies a shift from clear towards a brown water colour. This is because humic substances get washed out from the soil, dissolve in the water and get carried to rivers and lakes. Due to the darker water colour, less light passes through the water and reaches the bottom. This reduces photosynthesis, leading to lower energy production and lower macrophyte cover. Furthermore, fish can be affected in habitat availability and in feeding ability, as some rely on a good vision for feeding. Due to all these effects of browning, fish community responses are anticipated, but have rarely been studied so far. In this study I analysed data from 146 lakes in Sweden along a large water colour gradient from clear to brown lakes in order to find out how fish community biomass is influenced by water colour. Furthermore, I studied differences in how common different fish species are and mean body size and if they contribute to differences in community fish biomass between clear and brown lakes. I used absorbance at a specific wavelength as a measure of water colour and I tested the relationship between absorbance and different community measures for all 146 lakes in the study set. Specifically, community biomass (presenting the estimated summed weight of all fish caught in a lake), total fish abundance (presenting the number of fish individuals per lake), mean fish body length, length diversity (showing the variation in length between fish individuals), and species richness (giving the total number of species that occur in a lake) and species composition (the occurrence of different fish species), were analysed in relation to absorbance. The main result of my study was a negative relationship between fish community biomass and water colour, meaning less fish biomass in brown lakes. The lower community biomass is likely due to a lower biomass of the most common fish species, fewer fish individuals and a lower number of species and differences in fish community composition. Fish length could not explain the lower biomass in brown lakes. Other findings were that among clear lakes there was a higher variation in total fish abundance and biomass than dark lakes. When comparing lakes along the colour gradient to each other, values for highest biomass, highest number of individuals and number of species were much lower in darker lakes than in clear ones. Based on my results and considering that resource use and production are lower in dark lakes, I suggest a limitation of fish community biomass in brown lakes due to low resource availability. My study presents new insights into fish community responses to water colour, but I also argue that more research about browning effects on fish is needed. An improved understanding of ecological processes is important to make predictions and to develop management strategies to deal with the effects of continued water browning due to ongoing climate change.

Appendix

Table A1: Fish species and occurrence

Species	**Latin name**	**Number of lakes**
Perch	Perca fluviatilis	137
Northern Pike	Esox Lucius	119
Roach	Rutilus rutilus	104
Ruffe	Gymnocephalus cernuus	49
Bream	Abramis brama	34
Rudd	Rutilus erythrophthalmus	27
Bleak	Alburnus alburnus	24
Tench	Tinca tinca	23
Burbot	Lota lota	21
European Smelt	Osmerus eperlanus	19
Vendace	Coregonus albula	17
Minnow	Phoxinus phoxinus	13
Trout	Salmo trutta	13
Whitefish	Coregonus lavaretus	13
Arctic charr	Salvelinus alpinus	12
White bream	Abramis bjoerkna	8
Pikeperch	Sander lucioperca	6
Crucian carp	Carassius carassius	5
Alpine Bullhead	Cottus poecilopus	4
Bullhead	Cottus gobio	4
Eel	Anguilla anguilla	3
Greyling	Thymallus thymallus	3

Belica	Leucaspius delineatus	2
Ninespined stickleback	Pungitius pungitius	2
Brook trout	Salvelinus fontinalis	1
Zope	Abramis ballerus	1
Ide	Leuciscus idus	1
Spined loach	Cobitis taenia	1
Threespined stickleback	Gasterosteus aculeatus	1

Table A2: Statistical results for quantile regressions

metrics	Quantiles	R^1	Explanatory variable	Parameter (SE)	T	p
Community biomass	*0.1*	*0.016*	*Intercept*	*2.191 (0.146)*	*15.016*	*0.000*
			Absorbance	*-0.01 (0.006)*	*-1.504*	*0.135*
	0.5	*0.015*	*Intercept*	*3.107 (0.095)*	*32.86*	*0.000*
			Absorbance	*-0.021 (0.008)*	*-2.474*	*0.0145 **
	0.9	*0.053*	*Intercept*	*4.228 (0.14)*	*30.11*	*0.000*
			Absorbance	*-0.021 (0.009)*	*-2.384*	*0.018*
Total fish abundance	*0.1*	*0.014*	*Intercept*	*-1.585 (0.233)*	*-6.799*	*0.000*
			Absorbance	*-0.027 (0.017)*	*-1.615*	*0.109*
	0.5	*0.031*	*Intercept*	*-0.522 (0.127)*	*-4.096*	*0.000*
			Absorbance	*-0.038 (0.012)*	*-3.229*	*0.002 ***
	0.9	*0.024*	*Intercept*	*0.579 (0.199)*	*2.903*	*0.004*
			Absorbance	*-0.032 (0.016)*	*-1.965*	*0.051 **

Table A3: Environmental conditions and physical characteristics of the 146 study lakes.

Lake ID	**Lake name**	**Absorbance (a_{420})**	**Lake area (ha)**	**Mean depth**	**Temperature (°C)**	**Phosphorus**	**Pelagic sampling**
SE741340-153576	Njalakjaure	0.47	35	5.8	11.4	3.47	1
SE683337-133785	Ö. Särnamannasjön	0.47	28	1.9	12.7	4.50	0
SE758208-161749	Abiskojaure	0.48	282	12.8	12.2	3.80	1
SE683421-133742	N. Särnamannasjön	0.53	38	1.8	12.9	6.42	0
SE625182-146796	Skäravattnet	0.67	15	6	21.2	3.89	0
SE664620-148590	V. Skälsjön	0.77	43	6.6	19.2	3.71	1
SE751252-175433	Valkeajärvi	0.92	62		15.7	5.11	0
SE632023-131345	Härbillingen	0.92	13	5.1	20.2	5.60	0
SE633344-130068	Skärsjön	1.17	282	9.3	21.0	9.36	1
SE633959-144217	Skärlen	1.23	329	8.4	19.8	4.03	0
SE632515-146675	Hjärtsjön	1.24	137	3.4	19.2	3.94	0
SE655863-129783	Västra Solsjön	1.37	184	12.3	19.8	3.38	1
SE660749-161885	Fysingen	1.43	490	2	20.4	24.54	0
SE662682-132860	Örvattnet	1.47	80	9	18.2	4.97	1
SE615365-134524	Havgårdssjön	1.57	54	3.1	19.9	85.06	0
SE726381-152328	Magasjön	1.65	410		13.7	3.76	1
SE624718-141590	V. Hultasjön	1.73	8		20.8	6.14	0
SE615375-137087	Krageholmssjön	1.77	214	5	20.5	130.72	0
SE674570-141911	Rädsjön	1.95	58	8.8	17.6	3.70	1
SE644987-152393	Öjsjön	1.99	229	10	20.0	7.65	0
SE642122-148744	Glimmingen	2.00	175	10.4	19.9	4.83	0

Lake ID	Lake name	Absorbance (a_{420})	Lake area (ha)	Mean depth	Temperature (°C)	Phosphorus	Pelagic sampling
SE742829-183168	Pahajärvi	2.06	132	3.9	16.4	10.98	1
SE628606-133205	St Skärsjön	2.15	32	3.9	20.3	7.86	1
SE623304-145888	Lillasjön	2.20	10	2	22.2	9.60	0
SE624658-146086	Vitavatten	2.21	16	2.5	21.6	8.55	0
SE640364-129240	Stora Härsjön	2.26	257	14.1	20.3	4.31	1
SE663919-166636	Bottenfjärden	2.27	110	2.9	21.0	102.70	0
SE661866-130674	Norra Örsjön	2.32	55	8.6	18.3	3.88	0
SE617797-135339	Krankesjön	2.41	339	0.7	19.5	45.71	0
SE642489-151724	Allgjuttern	2.44	18	11.7	20.0	4.90	1
SE644964-128088	Stora Silevatten	2.45	5		20.1	4.00	0
SE662663-164643	Kundbysjön	2.47	26		18.9		0
SE658086-130264	Bysjön	2.58	113	7.4	18.9	12.51	1
SE653737-125017	Ejgdesjön	2.60	86	7	19.5		1
SE728744-162653	Vuolgamjaure	2.61	203	4.1	16.3	4.58	1
SE655209-126937	Stora Tresticklan	2.62	108		18.6	6.57	0
SE664197-149337	Dagarn	2.65	172	5.1	20.1	6.20	1
SE643361-130371	Gärsjön	2.65	8	2.6	20.6	5.60	0
SE664621-132502	Trehörningen	2.92	409	10.7	18.8	4.54	0
SE652707-159032	Björken	2.95	137	12.5	21.5	7.51	1
SE633025-142267	Fiolen	2.95	156	3.9	19.3	14.59	1
SE664410-136192	Översjön	2.99	38	11.4	18.5	6.46	0
SE661952-164005	Sparren	3.17	288	6.6	21.2	35.33	1

Lake ID	**Lake name**	**Absorbance (a_{420})**	**Lake area (ha)**	**Mean depth**	**Temperature (°C)**	**Phosphorus**	**Pelagic sampling**
SE659105-133982	Överudssjön	3.17	224	2.7	19.5	58.25	0
SE637121-151366	Tängersjö	3.24	11	3.1	20.3	7.43	0
SE651573-152481	Skärgölen	3.25	18	7	20.2	7.05	1
SE650061-142276	Humsjön	3.26	21	4	18.9	10.25	1
SE656804-128027	Motjärn	3.27	11		20.4	5.80	0
SE660688-164478	Tärnan	3.32	105	4.3	20.5	11.44	1
SE646293-126302	Granvattnet	3.39	18	1.6	20.1	22.41	0
SE656612-164132	Årsjön	3.48	21	3.8	20.7	4.95	0
SE690617-134197	Övre Fjätsjön	3.49	82		14.3	6.93	1
SE655587-158869	Stora Envättern	3.50	38	5.4	21.0	7.84	1
SE624038-143063	Örsjön	3.53	18	3.5	21.4	9.69	0
SE656419-164404	Stensjön	3.62	39	9.1	20.2	6.26	1
SE694411-155613	Kånkåstjärnen	3.76	11		18.5	6.80	0
SE658566-131495	Björnklammen	3.78	172	7.6	18.4	5.56	0
SE706083-132287	Stor-Björsjön	3.82	35	2.8	14.3	4.31	1
SE708512-152086	Degervattnet	3.85	158	5.1	18.3	5.73	1
SE624267-149857	Mossgöl	3.86	12	4	21.0	9.36	0
SE744629-167999	Jutsajaure	3.88	113	2.3	15.4	8.33	1
SE623175-146111	Blanksjön	3.90	19	4.9	21.7	7.06	1
SE661521-130182	Ulvsjön	4.42	49	10	18.2	7.11	1
SE637120-145525	Tångerdasjön	4.43	20	1.4	19.9	50.88	0
SE638725-146677	Fjärasjö	4.45	35	4.3	19.6	8.72	0

Lake ID	**Lake name**	**Absorbance (a_{420})**	**Lake area (ha)**	**Mean depth**	**Temperature (°C)**	**Phosphorus**	**Pelagic sampling**
SE691365-156127	V. Rännöbodsjön	4.53	48	6.2	20.4	12.59	1
SE690345-149315	Tväringen	4.60	161	4.9	17.9	4.66	0
SE680235-141799	Bösjön	4.88	114	4.2	16.4	4.36	1
SE683673-154083	Stensjön	4.93	59	4.3	19.4	5.78	1
SE718284-148654	Mellan-Rissjön	5.33	149		15.7	6.84	1
SE663216-148449	Lien	5.35	149	7.8	19.9	5.05	1
SE641603-144848	Försjön	5.35	163	5.7	19.3	7.18	0
SE645289-128665	Fräcksjön	5.37	28	4.1	20.8	10.09	1
SE634447-144024	Holmeshultasjön	5.41	64	5	19.2	10.48	0
SE692866-154650	Gransjön	5.44	38	7	19.5	6.05	0
SE711365-171748	Täftesträsket	5.58	242	4.3	18.6	10.63	0
SE635878-137392	Hagasjön	5.75	11	3.7	19.5	8.69	0
SE654508-127219	St Vrångstjärnet	5.83	10		20.2	5.30	0
SE634180-133441	Nässjön	6.40	52	2.7	19.9	16.69	0
SE656590-164240	Långsjön	6.40	9	3.8	20.3	6.19	0
SE625612-138546	Svanshalssjön	6.77	10	4.3	20.6	17.72	0
SE669097-133744	Stor-Hässlingen	7.02	88	5.7	18.5	6.43	0
SE718898-170673	Finnforsbodträsket	7.11	69		17.2	21.27	0
SE624486-141154	Skäravattnet	7.34	33	3	19.9	24.37	0
SE663532-148571	Övre Skärsjön	7.45	169	6.1	19.3	6.31	1
SE713404-172465	Bjännsjön	7.48	48	1.7	18.4	10.67	0
SE707669-170020	Lill-Bursjön	7.52	10	1.4	19.1		0

Lake ID	Lake name	Absorbance (a_{420})	Lake area (ha)	Mean depth	Temperature (°C)	Phosphorus	Pelagic sampling
SE635334-135239	Majsjön	7.52	296	8	19.4	8.97	0
SE695220-143383	Stor-Backsjön	7.55	206	2.3	16.5	12.07	0
SE661566-134372	Rinnen	7.61	464	4.8	20.0	13.85	0
SE624015-143187	Stora Ålagylet	7.65	4		21.4		0
SE665138-164175	Norrsjön	7.66	190	4.4	20.0	25.27	0
SE708619-162132	Remmarsjön	7.70	140	5	18.2	9.82	1
SE698918-158665	Valasjön	7.71	178	9	19.5	11.03	1
SE664614-136702	Stor-En	7.77	168	9.6	17.6	5.59	0
SE665144-139321	Stora Örsjön	7.84	137	5.1	18.6	9.00	0
SE693797-159720	Storsjön	7.99	309	2.6	19.8	15.03	0
SE623624-141149	Bäen	8.05	58	3.4	18.6	16.35	0
SE666268-142230	Skifsen	8.21	32	2.6	18.1	8.00	1
SE633209-141991	Gyslättasjön	8.26	32	2.8	19.4	14.23	1
SE709218-169710	Sidensjön	8.80	9	2.6	18.8	30.06	0
SE638317-138010	Stengårdshultasjön	9.13	489	7.1	19.0	7.59	1
SE663220-139381	Bosjön	9.16	124	7.3	19.1	8.18	0
SE664603-136484	Lill-En	9.16	14	9.9	17.9	6.89	0
SE652412-143738	Långsjön	9.21	67	4.2	20.3	11.89	1
SE666699-136103	Björklången	10.23	99	6.6	18.0	8.49	0
SE631309-134951	Södra Färgen	10.27	290	5.4	19.5	10.42	0
SE636930-137344	Klosjön	10.29	15	3.8	19.5	8.80	0
SE717734-173458	Brännvattsträsket	10.32	68	2.3	18.4	13.79	0

Lake ID	**Lake name**	**Absorbance (a_{420})**	**Lake area (ha)**	**Mean depth**	**Temperature (°C)**	**Phosphorus**	**Pelagic sampling**
SE630605-144655	Hinnasjön	10.88	26	1.4	19.5	18.71	0
SE631360-146750	Storasjö	11.10	37	1.8	19.2	17.39	0
SE721811-171800	Nyträsket	11.21	136		17.3	12.55	0
SE665175-157559	Siggeforasjön	11.52	76	4.2	19.1	14.11	0
SE723383-175441	Ytterträsket	11.60	10	2.8	17.7	14.48	0
SE626033-147550	Fersjön	11.66	8	1.3	21.2	20.48	0
SE670275-146052	Tryssjön	11.89	30	7.2	17.8	7.56	1
SE652902-125783	Rotehogstjärnen	11.90	16	3.6	19.5	14.23	0
SE655275-153234	Älgsjön	12.03	36	2.5	21.3	25.66	0
SE706041-157858	S. Bergsjön	12.16	36	4.8	18.7	12.99	0
SE672729-138082	Gipsjön	13.19	67	4.9	17.6	11.18	1
SE635072-137217	Hagsjön	13.23	24	4.6	19.7	8.50	0
SE647050-130644	Alsjön	13.64	6	5	19.8	12.92	0
SE663222-137322	Vågsjön	13.78	61		18.9	9.42	0
SE624178-134911	Lärkesholmssjön	13.95	76	4.2	19.4	20.33	1
SE683582-154935	Källsjön	14.06	24	7.1	19.2	9.55	1
SE706672-167201	Svartvattnet	14.66	5		18.1	15.53	0
SE637523-138710	Lomsjön	16.56	7	1.5	18.6	12.20	0
SE649314-149514	Geten	17.32	20	3.6	20.2	20.14	0
SE633989-140731	Älgarydssjön	17.49	34	1.4	19.7	27.44	0
SE622410-135589	Fåglasjön	17.61	60	0.9	19.5	68.38	0
SE638085-138862	Mossjön	18.21	49	2.1	19.7	24.82	0

Lake ID	Lake name	Absorbance (a_{420})	Lake area (ha)	Mean depth	Temperature (°C)	Phosphorus	Pelagic sampling
SE633738-142203	Stora Skärsjön	19.32	29	3.8	20.5	27.69	0
SE713180-153188	Djuphåltjärnen	19.35	6	3	14.7	31.25	0
SE629489-133906	Gyltigesjön	20.36	40	9.1	19.4	18.10	1
SE627443-149526	Brunnsjön	21.08	10	5.3	20.1	12.78	1
SE632231-136476	Harasjön	22.34	61	2.3	20.0	25.99	0
SE625269-140569	Hjärtasjön	24.28	20	2.7	21.1	21.00	0
SE668814-161417	Vikasjön	25.13	92	1.3	18.9	23.64	0
SE629880-135351	Knutsnabben	27.97	28	1.8	19.1	14.80	0
SE634496-146157	Vrången	28.02	54	1.2	19.7	30.48	0
SE629570-135470	Rammsjön	32.79	34	0.8	19.2	38.01	0
SE633573-134452	Hestrasjön	36.29	24	0.8	20.2	52.57	0
SE625911-138823	Liasjön	46.54	12	2.5	20.0	40.72	0
SE629643-142937	Brändasjö	53.61	14	1.9	20.2	32.00	0
SE630549-140714	Gölasjön	59.73	6	1.3	19.2		0
SE626898-138855	Farstusjön	66.61	22	1.2	20.5	51.93	0