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Factors behind the threshold-like changes in lake ecosystems along a water colour gradient: The effects of dissolved organic carbon and iron on euphotic depth, mixing depth and phytoplankton biomass

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Abstract

1. The effects of water colour, dissolved organic carbon (DOC), iron (Fe) and fetch on the mixing depth (Z_{mix}), euphotic depth (Z_{eu}) and phytoplankton biomass of lakes were studied to clarify the factors behind changes in lake productivity along a DOC gradient.
2. The study was conducted by field sampling 102 lakes in Finland. The lakes were situated mainly in forested areas.
3. At DOC concentrations below 15 mg/L, light attenuation was explained both by Fe and DOC, but at higher DOC concentrations the effect of Fe faded. For the absorption of different wavelengths of photosynthetic light, both DOC and Fe had a significant effect up to 475 nm, but for longer wavelengths only the effect of DOC was significant.
4. Both Z_{mix} and Z_{eu} decreased logarithmically with increasing DOC and water colour. Water colour was determined by DOC and Fe. Z_{mix} increased along with increasing fetch. Z_{mix} exceeded Z_{eu} when DOC concentration was >14.4 mg/L and water colour >106 mg Pt/L (platinum as chloroplatinate ion 3).
5. Above the 14.4 mg/L DOC threshold, the illuminated part of the mixed layer decreased logarithmically with increasing water colour, leaving an increasing part of the mixed epilimnion below the photosynthetic layer. Chlorophyll-*a* concentration showed a unimodal relationship with DOC, with the highest biomass occurring at DOC concentrations of 15.7–15.9 mg/L.
6. The results suggested that above DOC concentration 14 mg/L and water colour 106 mg Pt/L, both quality and quantity of light in the epilimnion restrict production by phytoplankton. This can explain the observed threshold-like changes in lake productivity along a DOC gradient.

KEYWORDS
dissolved organic carbon, euphotic depth, Fe, mixing depth, water colour

1 | INTRODUCTION

A large number of lakes are receiving increasing loads of dissolved organic carbon (DOC) from their catchments (Monteith et al., 2007; Roulet & Moore, 2006). The increasing flux of DOC has been induced by anthropogenic climate and land-use change (Asmala et al., 2019; de Wit et al., 2016; Weyhenmeyer et al., 2016). In some regions, decreasing sulphate deposition probably also has a role in the increasing loads of DOC (Meyer-Jacob et al., 2019; Monteith et al., 2007). The increasing DOC concentrations have fundamental impacts on the functioning of lake ecosystems because DOC affects the penetration of light into the water, thereby decreasing the euphotic depth (Z_{eu}) and increasing thermal water column stratification, with consequences for primary production, predator–prey interactions and competitive interactions between species (Estlander et al., 2010; Houser, 2006; Solomon et al., 2015). Additionally, the increasing flux of iron (Fe) from catchments is increasing the water colour of lakes and accelerating light attenuation in the water column (Kritzberg & Ekström, 2012; Weyhenmeyer et al., 2014).

Several studies have suggested that lake productivity and DOC concentration have a unimodal relationship. According to Solomon et al. (2015), numerous studies suggest that above DOC concentration thresholds of 10–14 mg/L the consumer production of lakes is severely reduced. A model formulated by Kelly et al. (2018) suggested that primary production peaks at DOC concentrations 6–15 mg/L and declines at higher concentrations. For northern lakes, in a study including benthic primary production, Seekell et al. (2015) reported a 4.8 mg/L threshold DOC concentration, below which the effect of DOC on primary production is positive and above which the effect is negative. It has been suggested that a change from nutrient limitation to light limitation is a factor behind such unimodal relationship between lake productivity and DOC (Seekell et al., 2015; Kelly et al., 2018). The existence of threshold DOC concentrations triggering the change have not, however, been comprehensively studied (Solomon et al., 2015). Studies spanning a wide DOC range are especially needed because the majority of studies on the relationship between DOC and light environment have focused on lakes with DOC concentrations <15 mg/L and studies in highly dystrophic lakes are rare. The light intensity changes that take place per unit of increasing DOC are most prominent at low DOC concentrations and low water colour (e.g., Eloranta, 1999; Hocking & Straškraba, 1999; Jones & Arvola, 1984), which may give the impression that only minor changes in lake productivity take place at high DOC concentrations. Lakes with high DOC concentrations are, however, numerous and studies conducted on high-colour lakes have demonstrated that substantial changes can take place in lake metabolism even at high DOC levels (Ask et al., 2009; Kelly et al., 2014). Additionally, the role of Fe is not well known. Through complexation with DOC, Fe can increase water colour per unit of DOC up to Fe concentration of 1–1.5 mg/L (Estlander et al., 2021; Weyhenmeyer et al., 2014). At higher concentrations, the additive effect of Fe on light absorption decreases, because DOC becomes saturated with Fe (Maloney et al., 2005; Xiao et al., 2013). Since numerous lakes have Fe concentrations <1 mg/L, increasing Fe can widely affect the water colour of fresh waters (Kritzberg & Ekström, 2012; Weyhenmeyer et al., 2014; Xiao & Riise, 2021). It is unknown, however, how Fe could contribute to the unimodal relationship between water colour and lake productivity.

Moreover, studies including high-colour lakes are needed, because human activities affecting fluxes of DOC and Fe, such as artificial ditching and peat mining, are usually concentrated in the catchments of lakes that have naturally high water colour and DOC concentration. In some regions, the largest increases in the concentration of organic carbon have occurred in lakes with the highest background concentrations (Estlander et al., 2021; Vuorenmaa et al., 2006). Considering biotic interactions, variations in light intensity at low light levels have strong effects, for instance, on the prey capture rate of visually orienting predators (Horppila et al., 2004; Richmond et al., 2004; Utne, 1997). Therefore, even small increases in DOC or Fe concentrations may be detrimental for predator–prey interactions, especially in lakes with high background water colour.

In this study, the effects of variable water colour, DOC and Fe concentrations on the light environment, mixing depth (Z_{mix}) and chlorophyll-*a* (Chl-*a*) concentration of lakes were studied by including a wide range of water colour (1.3–505.0 mg Pt/L [platinum as chloroplatinate ion 3]) and DOC concentrations (2.4–36.9 mg/L). With wide water colour and DOC gradients, the study brings new information on the roles of DOC and Fe as regulators of lake productivity together with nutrients and clarifies the factors behind the threshold-like changes taking place in lake productivity along a DOC gradient.

2 | METHODS

2.1 | Study lakes, water quality sampling and water analyses

The main data were collected from 102 lakes situated in southern and central Finland (Figure 1). The surface area of the lakes varied between 0.2 and 2,117.4 ha (Table 1). Forests covered 30.5%–98.5% (average 79.6%) and lakes 0%–13.8% (average 10.7%) of the catchments. The coverage of agriculture in the catchments was 0%–28.1% (average 2.8%). Estlander et al. (2021) showed that DOC and Fe concentrations of the study lakes depended strongly on catchment land use, especially on the density of artificial ditches in the catchment. The exact location and individual water quality characteristics of the lakes are presented in Table S1. Water samples (three replicates from each lake) for water quality analysis of the lakes were collected in 2019–2020 between 17 June and 9 July with a Limnos tube sampler (volume 2.8 L, Limnos) from 0.5 to 1 m depth. The samples were analysed for total phosphorus (P), total nitrogen (N), Fe, suspended solids (SS), DOC, water colour and Chl-*a*. Total P and total N concentrations were determined with a Lachat autoanalyser (QuickChem Series 8000; Lachat Instruments). DOC concentration was determined with a TOC-VCPH analyser (Shimadzu Corporation) following standard SFS-EN 1484 (Finnish Standards Association, 1997).

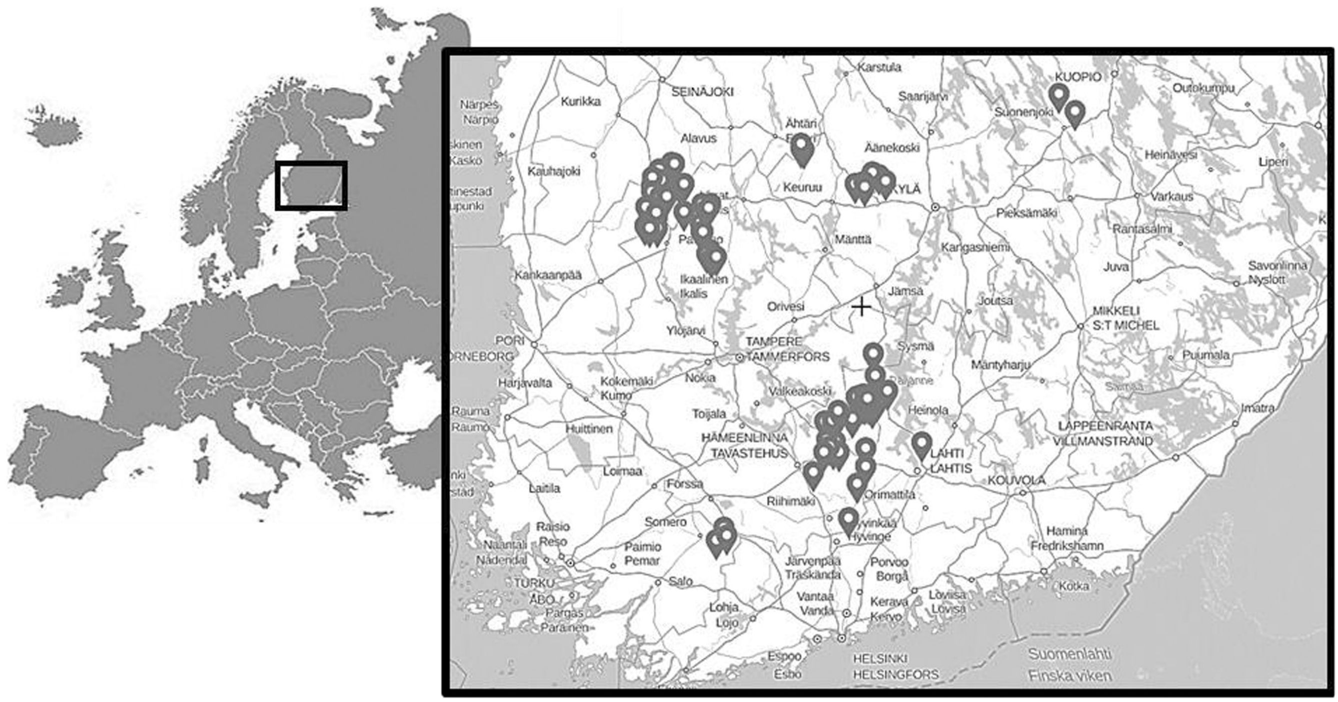

FIGURE 1 Locations of the study lakes. The lakes ($n = 102$) were situated in southern and central Finland and sampled in June–July 2019–2020.

TABLE 1 Minimum, average and maximum values of the main characteristics of the study lakes.

	Minimum	Average	Maximum
Lake area (ha)	0.2	72.7	2,117.4
Water colour (mg Pt/L)	1.3	141.4	505.0
DOC (mg/L)	2.4	15.8	36.9
Fe (mg/L)	0.01	0.76	3.5
Total P (μg/L)	5	22	81
Total N (μg/L)	190	534	1,733
Chl-*a* (μg/L)	1	14.2	161
SS (mg/L)	0.5	3.3	31.3
K_d (m^{-1})	0.54	4.1	12.4

Note: Water quality values are for 0.5–1 m depth.

Water colour was measured with a Shimadzu UV-1800 spectrophotometer as the absorbance of light at the 410 nm wavelength and converted to mg Pt/L according to the standard SFS-EN ISO 7887 (Finnish Standards Association, 2011). Fe was analysed from one of the replicate samples of each lake using an atomic absorption spectrophotometer (SpectrAA 220FS; Varian) according to standard SFS 3044 (Finnish Standards Association, 1980). The concentration of SS was determined after filtration through GF/C filters and drying at 105°C. Chl-*a* concentration was analysed with an F-4000 fluorescence spectrophotometer (Hitachi Ltd) with excitation and emission wavelengths of 435 and 671 nm after filtration on Whatman GF/C filters and extraction with ethanol.

2.2 | Temperature and light intensity measurements

The vertical profile of water temperature in each lake was determined with a 6820 CTD sonde (YSI Inc.). Z_{mix} was determined as the layer above the depth with maximum temperature change (Keller et al., 2006). Vertical variation in the intensity of photosynthetically active radiation (PAR, 400–700 nm) in the water column was measured with an LI-1400 data logger equipped with an LI-192SA quantum sensor (LI-COR Biosciences). The light attenuation coefficient K_d was calculated for each lake with the equation (Eloranta, 1999; Scheffer, 1998):

$$K_d = \frac{\ln \frac{I_0}{I_Z}}{Z}$$

where I_0 and I_Z are light intensities just below the surface and at depth Z (0.5 m), respectively.

Mean epilimnetic irradiance ($E\%$) as a proportion of surface light was calculated with the equation (Sterner, 1990; von Einem & Granéli, 2010):

$$E\,\% = \frac{100\left(1 - e^{-K_d Z_{mix}}\right)}{K_d Z_{mix}}$$

Z_{eu} was calculated with the equation (Brown, 1984; Scheffer, 1998):

$$Z_{eu} = \frac{4.6}{K_d}$$

2.3 | Spectral light absorption measurements

Additionally, to clarify the role of Fe and DOC in the attenuation of light, the absorbance of different light wavelengths (200–750 nm) was measured (Shimadzu UV-1800 spectrophotometer) from samples taken with a tube sampler for this purpose from four of the study lakes during summer 2021. The measurements were conducted because variable results on the role of Fe versus DOC in light absorption at different wavelengths have been reported. Fe strongly absorbs ultraviolet (UV) radiation but also affects the attenuation of PAR wavelengths, and the effect of Fe in relation to DOC may depend on the quality of the water and organic matter (Maloney et al., 2005; Pullin et al., 2007; Xiao et al., 2015). The chosen lakes, Kärppäjärvi, Käkilammi, Neva-Lyly and Valkea Mustajärvi, had contrasting concentrations of DOC and Fe, which facilitated the evaluation of the effects of Fe versus DOC. Samples for absorption measurements were collected from the epilimnion and hypolimnion at different times during the summer (Käkilammi and Valkea Mustajärvi seven times [7 June, 21 June, 5 July, 19 July, 2 August, 21 August, 9 September], Kärppäjärvi and Neva-Lyly twice [14 June, 10 August]) to cover a wide variety of DOC–Fe combinations (each day three replicate samples from each lake and depth).

2.4 | Data analysis

The effects of DOC, Fe, total P, Chl-*a* and SS on water colour and K_d in the 102 study lakes were studied with multiple linear regression (Thrane et al., 2014). Before the analyses, data were ln-transformed to improve normality. To evaluate the effects of Fe in different lakes, linear regression analyses were conducted with different subsets of data (determined by the upper limit of DOC concentration: 2.9–10.0, 2.9–12.5, 2.9–15.0, 2.9–17.5, 2.9–20.0, 2.9–25.0 and 2.9–37.0 mg/L) by using either DOC alone or DOC and Fe together as predictors and water colour and K_d as dependent variables.

Additionally, the effects of DOC, Fe and fetch on Z_{mix}, and the effect of DOC and Fe on the absorption of different wavelengths were analysed with multiple linear regression (ln-transformed data). Lake fetch was determined as the square root of the lake area (Von Einem & Granéli, 2010). Lake size must be included in the analyses, because it affects the mixing depth at a given light extinction (e.g., Kelly et al., 2018). The effect of water colour on Z_{mix} and Z_{eu}, and the effect of DOC on total P, total N and E% were studied with simple linear regression (von Einem & Granéli, 2010). Analyses for Z_{mix}, Z_{eu} and E% were conducted for lakes that were deep enough to show temperature stratification ($n = 67$) and the analyses for spectral light absorption for the samples collected from the four chosen lakes (Käkilammi, Kärppäjärvi, Neva-Lyly, Valkea Mustajärvi). To explore the possible unimodal relationship between phytoplankton biomass and water quality, the effects of DOC, water colour and total P on Chl-*a* concentration were examined with second-order polynomial regression (ln-transformed data). In the analysis, Chl-*a* concentration was calculated per unit area of epilimnion to account for between-lake variability in thermocline depth. The analyses for Chl-*a* were performed for the stratifying lakes to facilitate comparisons with the effects of Z_{mix}:Z_{eu}.

3 | RESULTS

3.1 | Water quality variation and factors contributing to water colour

The variation in the water quality characteristics was wide among the study lakes. Water colour varied between 1.3 and 505.0 mg Pt/L and DOC concentration between 2.4 and 36.9 mg/L (Table 1). The concentrations of total P (5–81 µg/L), total N (190–1,733 µg/L) and Chl-*a* (1–161 µg/L) reflected conditions from oligotrophy to eutrophy. Both total P and total N increased linearly together with DOC (P: $F_{1,100} = 67.80$, $R^2 = 0.4040$, $p < 0.001$; N: $F_{1,100} = 88.12$, $R^2 = 0.4684$, $p < 0.001$). Fe concentration varied from 0.01 to 3.5 mg/L. The large variation in water quality was seen in the K_d values, which ranged from 0.54 to 12.4 m^{-1} (Table 1). Water colour was strongly determined by DOC, which alone explained 91.6% of the colour variation (Table 2). The effect of Fe on colour also was significant, and alone it explained 62.8% of water colour fluctuations. DOC and Fe together covered 93.3% of the colour variation. Lake fetch, total P, Chl-*a* and turbidity were insignificant as predictors of water colour (Table 2). Analysis with different DOC ranges showed that the positive effect of Fe on the R^2-value of the regression predicting water colour was strong at DOC concentrations <15 mg/L and decreased considerably with higher DOC concentrations (Figure 2a).

3.2 | Factors affecting light attenuation (K_d) and mixing depth (Z_{mix})

With the whole set of study lakes, DOC explained 73.2% of the variation in K_d (Table 2). The effect of Fe on K_d was insignificant when it was added as a predictive variable together with DOC (Table 2). A more detailed analysis revealed, however, that when Fe was added to the regression with DOC, it considerably increased the R^2-value at DOC concentrations <15 mg/L, but at higher DOC concentrations no effect of Fe was detected (Figure 2b). Fetch, Chl-*a* and SS had no effect on K_d, but total P concentration had a slight positive effect (Table 2).

In the spectral light absorption measurements from the four selected lakes, DOC concentration varied from 5.3 to 37.8 mg/L, Fe concentration from 0.1 to 4.7 mg/L and the Fe:DOC ratio from 0.015 to 0.20 (Table S2). Both DOC and Fe had a highly significant effect on absorption for wavelengths from 350 to 475 nm (Table 3). At wavelengths >475 nm, the effect of DOC was significant and the effect of Fe insignificant (Table 3).

In lakes that showed temperature stratification, Z_{mix} was mainly determined by DOC concentration, which had a strong negative effect and alone explained 51.1% of the variation in Z_{mix} (Table 2). Fetch had a significant positive effect on Z_{mix} (Table 2). DOC and fetch together explained 71.3% of the variation in Z_{mix} (Table 2). The effect of Fe on Z_{mix} was insignificant (Table 2).

TABLE 2 Regression equations and their R^2-values for predicting water colour, light attenuation coefficient (K_d) and mixing depth (Z_{mix}) from concentrations of DOC, Fe, total P (TP), Chl-*a* and SS, and fetch.

Equation	R^2
Water colour ($n = 102$)	
ln(colour) = 1.8885 × ln(DOC)** − 0.3753	0.9157
ln(colour) = 0.7204 × ln(Fe)** + 5.1464	0.6282
ln(colour) = 1.6064 × ln(DOC)** + 0.1768 × ln(Fe)** + 0.4977	0.9331
ln(colour) = 1.8836 × ln(DOC)** − 0.0261 x ln(fetch) − 0.048	0.9178
ln(colour) = 1.9714 × ln(DOC)** − 0.1108 × ln(TP) − 0.2716	0.9183
ln(colour) = 1.9005 × ln(DOC)** − 0.0147 × ln(Chl-*a*) − 0.3745	0.9159
ln(colour) = 1.9029 × ln(DOC)** − 0.0316 × ln(SS) − 0.3855	0.9163
Light attenuation coefficient ($n = 102$)	
ln(K_d) = 1.0655 × ln(DOC)** − 1.5966	0.7319
ln(K_d) = 1.0402 × ln(DOC)** + 0.0159 × ln(Fe) − 1.5183	0.7322
ln(K_d) = 1.0589 × ln(DOC)** − 0.0349 × ln(fetch) − 1.1583	0.7415
ln(K_d) = 0.9415 × ln(DOC)** + 0.1657 × ln(TP)* − 1.7518	0.7465
ln(K_d) = 1.0368 × ln(DOC)** + 0.0349 × ln(Chl-*a*) − 1.5984	0.7341
ln(K_d) = 1.0680 × ln(DOC)** − 0.0057 × ln(SS) − 1.5984	0.7319
Mixing depth ($n = 67$)	
ln(Z_{mix}) = −0.7524 × ln(DOC)** + 2.2480	0.5111
ln(Z_{mix}) = −0.8253 × ln(DOC)** + 0.0518 × ln(Fe) + 2.4903	0.5150
ln(Z_{mix}) = −0.6744 × ln(DOC)** + 0.1677 × ln(fetch)** + 0.1242	0.7125
ln(Z_{mix}) = 0.2061 × ln(fetch)** − 2.0628	0.3128
ln(Z_{mix}) = −0.6156 × ln(DOC)** + 0.1720 × ln(fetch)** − 0.0403 × ln (Fe) − 0.1201	0.7148

Note: Statistically significant parameters are indicated with asterisks (**, $p < 0.01$; *p, < 0.05).

3.3 | The effects of DOC and water colour on euphotic depth and mixing depth

The effect of DOC on Z_{eu} and Z_{mix} followed a logarithmic function (Figure 3). Both effects were highly significant (Z_{eu}: $F_{1,65} = 185.13$, $R^2 = 0.7401$, $p < 0.001$; Z_{mix}: $F_{1,65} = 72.90$, $R^2 = 0.5286$, $p < 0.001$). Z_{mix} exceeded Z_{eu} when DOC concentration was >14.4 mg/L (Figure 3). The effect of water colour on Z_{eu} was described by the equation $\ln(Z_{eu}) = -0.5355 \times \ln(\text{colour}) + 2.7389$ ($F_{1,65} = 186.66$, $R^2 = 0.7417$, $p < 0.001$), while the effect of water colour on Z_{mix} followed the equation $\ln(Z_{mix}) = -0.3884 \times \ln(\text{colour}) + 2.0528$ ($F_{1,65} = 71.65$, $R^2 = 0.5243$, $p < 0.001$). Z_{mix} exceeded Z_{eu} when water colour was >106 mg Pt/L.

When the difference between Z_{mix} and Z_{eu} was presented as a proportion of the mixed layer left below Z_{eu} along a colour gradient,

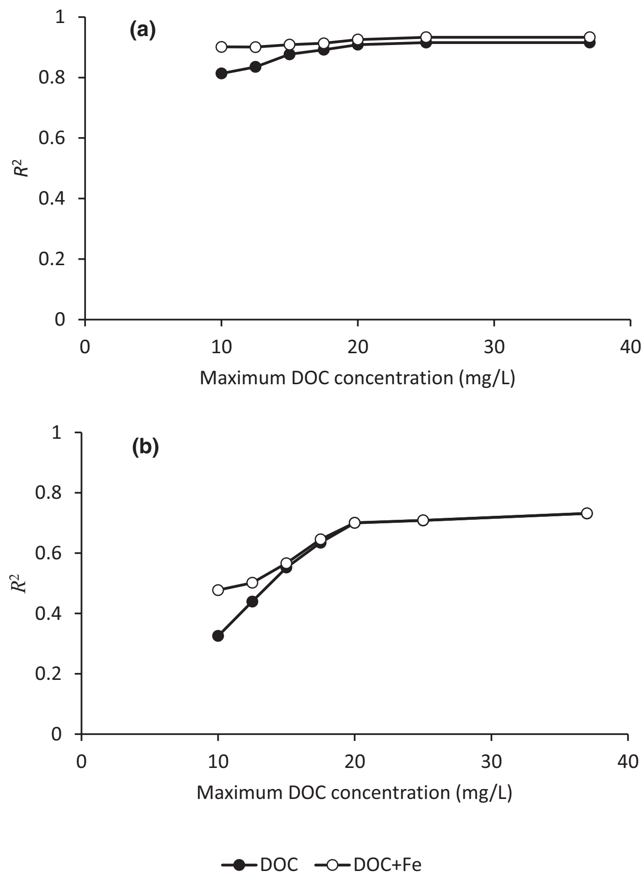

FIGURE 2 R^2-values of the regression equations predicting (a) water colour and (b) light attenuation coefficient (K_d) with DOC alone or DOC and Fe together as predictors, and with different maximum DOC concentrations in the studied set of lakes.

the proportion started to increase logarithmically when DOC concentration exceeded 106 mg Pt/L and DOC concentration exceeded 14.4 mg/L (Figure 4). The development of the proportion of Z_{mix} below the euphotic depth at DOC concentrations above 14.4 mg/L was described by the function $y = 24.365 \times \ln(\text{colour}) - 64.147$. $E\%$ decreased significantly with increasing water colour ($F_{1,65} = 5.74$, $R^2 = 0.0811$, $p = 0.0195$; Figure S1). DOC alone also had a significant negative effect on $E\%$ ($F_{1,65} = 5.62$, $R^2 = 0.080$, $p = 0.0207$). However, owing to large variation in $E\%$ with a given water colour and DOC, especially at low colour and DOC values, R^2-values were low. When lake fetch together with water colour was used as a predictor of $E\%$, the model performance improved ($F_{2,64} = 11.02$, $R^2 = 0.2561$, $p < 0.001$).

3.4 | The dependence of Chl-*a* concentration on DOC, water colour and P

There was a clear unimodal variation in Chl-*a* concentration along a DOC gradient (Figure 5). The relationship between Chl-*a* concentration of the lakes and DOC was described by a second-order polynomial function $\ln(\text{Chl-}a) = -0.0074 \times \text{DOC}^2 + 0.236 \times \text{DOC} + 8.2457$ ($F_{2,64} = 20.95$, $p < 0.001$). According to the equation, the highest

TABLE 3 Results of the regression analyses for the effects of DOC and Fe on light absorption at different wavelengths.

Wavelength (nm)	$F_{2,33}$	R^2	*p* (DOC)	*p* (Fe)
300	2,576.19	0.9936	<0.0001	0.0001
350	2,979.56	0.9945	<0.0001	<0.0001
400	2,196.08	0.9925	<0.0001	<0.0001
450	1,193.39	0.9864	<0.0001	0.0097
475	925.65	0.9825	<0.0001	0.0251
500	713.44	0.9774	<0.0001	0.0753
550	435.89	0.9635	<0.0001	0.5423
600	331.28	0.9526	<0.0001	0.8933
650	242.47	0.9363	<0.0001	0.7000
700	226.53	0.9321	<0.0001	0.3098
750	150.77	0.9014	<0.0001	0.2020

Note: The measurements were made with water sampled from lakes Valkea Mustajärvi (DOC 5.3–6.6 mg/L, Fe 0.1–0.7 mg/L), Neva-Lyly (DOC 13.3–13.8 mg/L, Fe 0.2–0.7 mg/L), Kärppäjärvi (DOC 22.6–27.9 mg/L, Fe 2.6–4.7 mg/L) and Käkilammi (DOC 27.3–37.8 mg/L, Fe 1.0–2.0 mg/L).

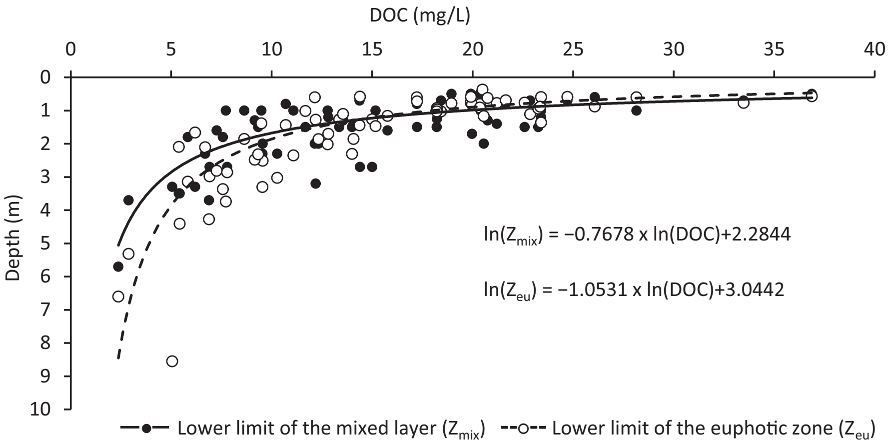

FIGURE 3 Effect of DOC concentration on the mixing depth (Z_{mix}, solid line) and euphotic depth (Z_{eu}, dashed line) in the stratified study lakes.

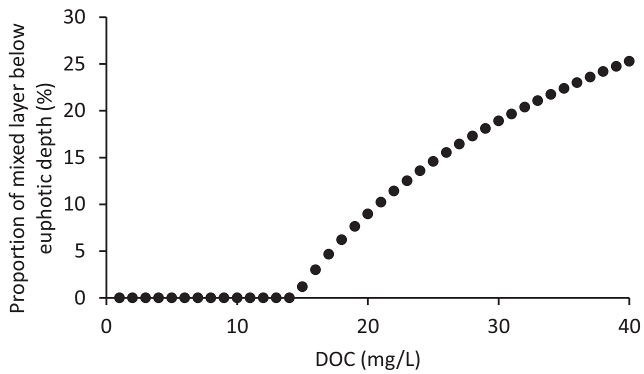

FIGURE 4 Effect of DOC concentration on the proportion of the mixed layer situated below the euphotic depth (Z_{eu}).

Chl-*a* concentration was on average reached at DOC concentration 15.9 mg/L. When water colour was used as a predictor instead of DOC, the function had the form ln(Chl-*a*) = −0.00004 × Colour^2 + 0.0114 × Colour + 9.2131 ($F_{2,64}$ = 32.06, $p < 0.001$), and the location of the peak Chl-*a* concentration at the DOC gradient decreased slightly (water colour = 142.5 mg Pt/L, DOC = 15.7 mg/L). With total P as a predictor for Chl-*a*, the second-order model (ln(Chl-*a*) = −0.00236 × P^2 + 0.1245 × P + 8.4534) also was significant ($F_{2,64}$ = 5.53, p = 0.0061). According to the model, the highest Chl-*a* concentration occurred at P concentration 26 μg/L. When analysed by linear regression with all the stratified lakes included in the analysis, Chl-*a* per unit lake area showed significant dependence on P, but with a low R^2-value ($F_{1,65}$ = 4.95, R^2 = 0.071, p = 0.030). When only lakes with DOC concentration lower than the 14.4 mg/L threshold ($Z_{mix} = Z_{eu}$) were included (n = 35), the performance of the linear model predicting Chl-*a* from P improved substantially ($F_{1,34}$ = 42.03, R^2 = 0.5602, $p < 0.001$).

4 | DISCUSSION

Following the results of previous studies, water colour had a strong negative effect on both Z_{eu} and Z_{mix} (Hocking & Straškraba, 1999; Jones & Arvola, 1984; Pérez-Fuentetaja et al., 1999). The effect of water colour was stronger for K_d than Z_{mix}. This was explained by the effect of fetch, which was significant for Z_{mix} but insignificant for K_d. Also for Z_{mix}, DOC was, however, a more important regulator than fetch. The study lakes were mostly small, whereas lake size becomes a more important regulator of Z_{mix} than water transparency

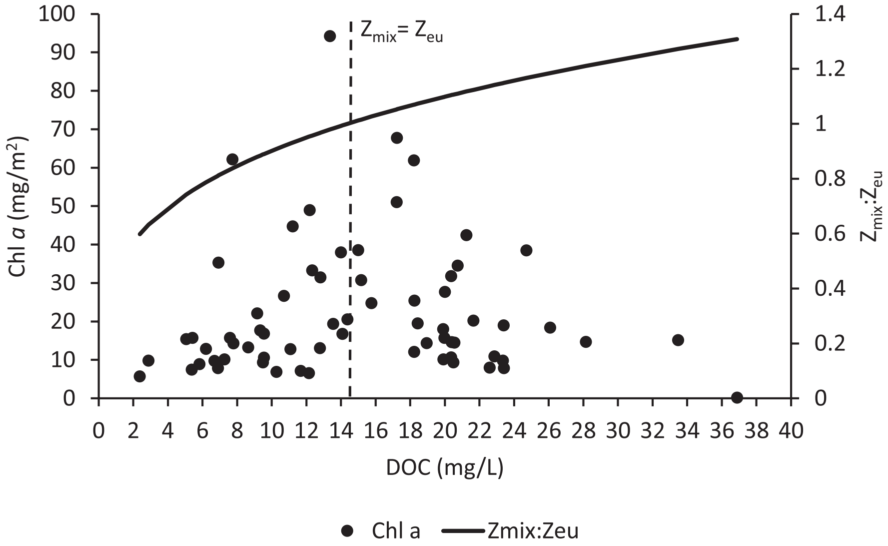

FIGURE 5 Chlorophyll-*a* concentration (left axis) along a DOC gradient and the effect of DOC on the Z_{mix}:Z_{eu} relationship (right axis) in the stratifying study lakes. The solid line indicates the relationship of Z_{mix} and Z_{eu} (Z_{mix}:Z_{eu}) along the DOC gradient. It was calculated as the difference between the two logarithmic curves presented in Figure 3. The dashed vertical line indicates the DOC concentration, where $Z_{mix} = Z_{eu}$.

usually only in large lakes (Fee et al., 1996; Houser, 2006; Keller et al., 2006). Von Einem and Granéli (2010) found that even for small lakes (<3.5 km^2) fetch instead of DOC was the main regulator of Z_{mix}, but that was explained by the strong maritime influence on the weather conditions compared with the more continental location of the present study lakes.

In a study of Finnish forest lakes, Jones and Arvola (1984) reported that phytoplankton were not subject to large changes in light intensity with increasing DOC, because Z_{mix} decreased together with Z_{eu}, and the effective light climate remained relatively constant along a DOC gradient. According to our results, *E*% decreased with increasing DOC and water colour, although the variation was large a result of the effect of fetch on Z_{mix}. Likewise, Von Einem and Granéli (2010) found a strong negative effect of DOC concentration on *E*%. In the study lakes of Jones and Arvola (1984), the DOC concentration range was 4.6–14.1 mg/L, whereas it was 2.4–36.9 mg/L in the present study and 3.7–26.9 mg/L in the study by Von Einem and Granéli (2010). Our study demonstrated that Z_{mix} exceeded Z_{eu} at DOC concentrations >14.4 mg/L. Thus, the different results compared with Jones and Arvola (1984) were explained by the difference in the DOC concentration range of the study lakes. This was confirmed by analysing the dependence of *E*% on DOC with the present data but including only lakes with DOC concentration between 4 and 14 mg/L. With this subset of lakes, the effect of DOC on *E*% was insignificant (p = 0.4080). This underlined the importance of including data from high-colour lakes. With a wide water-colour range, the negative effect of high-water colour on lake productivity is revealed, and the unimodal relationship between phytoplankton biomass and water colour can be detected.

In those lakes with lowest water colour, Z_{eu} exceeded Z_{mix}, which is common in small boreal lakes with high transparency (Eloranta, 1999). In highly dystrophic lakes, the epilimnion often is thicker than the euphotic zone, because along a DOC gradient Z_{eu} decreases more steeply than Z_{mix} (Arvola et al., 1996; Eloranta, 1999; Houser, 2006). In our study lakes, Z_{mix} exceeded Z_{eu} when DOC concentration was >14.4 mg/L, which was in line with the range of the threshold DOC concentrations, above which substantial reductions in lake productivity, including secondary production, have been observed (Bergström & Karlsson, 2019; Kelly et al., 2018; Solomon et al., 2015). For lakes in northern Sweden, Bergström and Karlsson (2019) observed the highest phytoplankton biomass at DOC concentration of 11 mg/L. Compared with the present study lakes, the lakes in Bergström and Karlsson (2019) were less productive with total P concentration <20 μg/L and total N concentration <550 μg/L, and on average smaller with a maximum area of 10 ha. Based on lake size, a higher DOC concentration threshold for light limitation could be expected compared with the present study lakes, because with a given DOC concentration Z_{mix} increases with lake size (e.g., Kelly et al., 2018). However, size alone does not determine the wind exposure of lakes, but catchment characteristics also have a role. It is possible that the northern boreal and arctic lakes have more open and wind-exposed catchments than the present study lakes that were mostly surrounded by a dense forest. Differences in phytoplankton species composition, in DOC quality (e.g., aromaticity) or in fish density (through effects on zooplankton) also may contribute to the difference between the study results (Bergström & Karlsson, 2019; Kelly et al., 2018, Lenard et al., 2018). Our finding on the DOC threshold was in close agreement with that of Kelly et al. (2018), whose model-based study suggested that the highest phytoplankton production in 0.1–1 km^2 lakes takes place at DOC concentrations around 15 mg/L.

The highest Chl-*a* concentrations in the study lakes occurred at DOC concentrations close to the Z_{mix} = Z_{eu} threshold, which supported the strong role of Z_{mix}:Z_{eu} in regulation of phytoplankton biomass. If $Z_{mix} > Z_{eu}$, phytoplankton will spend part of their life in circumstances where respiration exceeds photosynthesis (von Einem & Granéli, 2010). The larger the difference between Z_{mix} and Z_{eu}, the longer periods that phytoplankton will spend below the productive layer (Grobbelaar, 1990; Reynolds, 2006). Therefore, phytoplankton production tends to decrease with increasing Z_{mix}:Z_{eu}, and an unfavourable Z_{mix}:Z_{eu} ratio reduces the food base of the lake (Alpine & Cloern, 1988; Grobbelaar, 1985; von Einem & Granéli, 2010). Our data demonstrated that the illuminated part of Z_{mix} started to decrease logarithmically when DOC concentration exceeded 14.4 mg/L. The Z_{mix}:Z_{eu} ratio provides an estimate of the proportion of the population that is below the productive layer (Khanna et al., 2009). Thus, when the DOC concentration of the study lakes increases, for instance, from 15 to 30 mg/L, the mixed zone depth below the euphotic layer increases from 1.8% to 18.7%, which may be unfavourable for phytoplankton. Therefore, substantial changes in lake ecosystems can occur along the DOC gradient even at high DOC concentrations. Variable estimates for Z_{mix}:Z_{eu} ratios critical for phytoplankton production have been presented (Alpine & Cloern, 1988; Grobbelaar, 1990; Khanna et al., 2009), but it must be taken into account that in sheltered forest lakes water mixing often is weak. This is notable, because the deeper that Z_{mix} is in relation to Z_{eu}, the more important mixing is for photosynthesis (Reynolds, 2006). It must also be taken into account that when $Z_{mix}<Z_{eu}$, phytoplankton production can take place below the epilimnion (Obrador et al., 2014; Stefan et al., 1995). Thus, epilimnetic sampling could result in underestimated phytoplankton biomass in low-colour lakes. Obrador et al. (2014) reported that in such cases epilimnion-based areal estimates of primary production could deviate from the true values by 60%. The study lakes in Obrador et al. (2014) had DOC concentrations 2.97–4.79 mg/L, total P concentrations 19.5–102 μg/L and Chl-*a* concentrations 5.3–65 μg/L. Our lakes with a similar DOC concentration had substantially lower total P concentration (<10 μg/L) and Chl-*a* concentration (<3 μg/L). Thus, in the present study lakes the error resulting from exclusion of phytoplankton below the epilimnion was probably smaller than predicted in Obrador et al. (2014). In some of the most transparent lakes of the present dataset, slight increases in oxygen saturation in the metalimnion were observed, indicating metalimnetic primary production, but only in one case did the metalimnetic increase in oxygen saturation exceed 5%.

Bergström and Karlsson (2019) found a unimodal relationship between phytoplankton biomass and nutrients, which was explained by the shift from nutrient limitation to light limitation. At high DOC concentrations, phytoplankton biomass declined along a DOC gradient owing to light limitation even with the increasing availability of the limiting nutrient. Our data showed signs of a similar relationship between phytoplankton biomass and the limiting nutrient (P). Chl-*a* was tightly dependent on P concentration at low DOC concentrations, but at high DOC levels the effect of P became weaker. The estimated DOC concentration for maximum Chl-*a* (15.7–15.9 mg/L) was somewhat higher than DOC concentration for $Z_{mix} = Z_{eu}$ (14.4 mg/L). This difference can be attributed to the adaptability of phytoplankton. With decreasing light availability, the dominance of species with greater light-use efficiency may increase, and the photosynthetic pigment content of phytoplankton cells may change facilitating a more efficient use of low light (Desortová, 1981; Diehl et al., 2002; Edwards et al., 2013; Lenard et al., 2018). The mobile flagellated species may perform diurnal migrations, but usually they occupy the epilimnion during the day and stay deeper at night (Pęczuła et al., 2014; Salonen et al., 1993). Thus, their biomass there was not underestimated by samples taken in the daytime.

Our results supported the conclusions that substantial changes in phytoplankton production of lake ecosystems can take place when a certain threshold DOC concentration is exceeded (Kelly et al., 2018; Solomon et al., 2015). However, in addition to DOC, Fe also played an important role. Fe forms complexes with DOC, explaining why Fe concentration increased together with DOC (Kritzberg & Ekström, 2012; Maloney et al., 2005). The high R^2-value of Fe alone as a predictor of water colour was thus partly due to its association with DOC. When the Z_{mix}:Z_{eu} threshold was predicted with DOC, the threshold concentration was 14.4 mg/L. When water colour was used as a predictor, the threshold was 106 mg Pt/L, which corresponded to a DOC concentration of 13.0 mg/L. The difference was a result of the effect of Fe. Because water colour includes the effect of Fe together with DOC, Z_{mix}:Z_{eu} threshold was reached at a lower DOC concentration with water colour than with DOC as a predictor.

When exploring the effects of Fe on the light environment, the studied colour and DOC ranges were of importance. Thrane et al. (2014) concluded that a larger part of the variation in K_d was explained when Fe was included in the analyses together with DOC. The maximum DOC concentration (12.3 mg/L) in Thrane et al. (2014) was, however, considerably lower than in the present study. Our analysis revealed that the effect of Fe on K_d was strong at low DOC concentrations but faded at DOC concentrations >15 mg/L. This can be explained by the strong absorption of short-wavelength light by Fe (Maloney et al., 2005). For instance, the absorption of 410 nm light increases linearly with Fe concentration (Xiao et al., 2015). Although Fe concentration increased together with DOC also at high DOC concentrations, it had no additive effect on K_d because short wavelengths were absent. The spectral absorption analyses confirmed that the effect of Fe was particularly strong for UV and short wavelengths of PAR (cf. Maloney et al., 2005; Pullin et al., 2007). The selective effect of Fe on light absorption also would explain why Fe had a significant effect on water colour (measured as absorption of 410 nm light) but no effect on the K_d of PAR light when the whole DOC range of the study lakes was included in the analyses. However, the effect of Fe on the absorption of short wavelength light probably did not solely explain why the effect of Fe on K_d faded at high DOC concentrations. A further explanation was the saturation of organic matter with Fe, a phenomenon described also for the present study lakes (Brezonik et al., 2019; Estlander et al., 2021; Weyhenmeyer et al., 2014). Because the effect of Fe on light absorption is dependent on its complexation with DOC, the effect of Fe additions decreases after the saturation of DOC with Fe at Fe concentrations >1 mg/L (Weyhenmeyer et al., 2014). Accordingly, DOC concentrations of 15–20 mg/L, where the effect of Fe on K_d faded, corresponded to Fe concentrations of 0.8–1 mg/L.

The results indicated that two different phases in the development of epilimnetic circumstances occurred when DOC concentration of the lakes increased. Firstly, at DOC concentration <15 mg/L, nutrients stimulated the growth of phytoplankton biomass, while Fe had a strong effect on the attenuation of short-wavelength light. This was notable, because the blue part of PAR is especially important for photosynthesis as it is in the peak absorption range of photosynthetic pigments (Kirk, 1976; Thrane et al., 2014). Secondly, at DOC concentration >14.4 mg/L and water colour >106 mg Pt/L, Z_{mix} became deeper than Z_{eu}, leaving a proportion of the mixed layer below the euphotic depth. Above this threshold, the proportion of epilimnion below Z_{eu} increased steeply with increasing DOC and water colour. Hence, above 14–15 mg/L DOC concentration, both the quality and quantity of light in the epilimnion started to restrict production by phytoplankton. The threshold water colour and DOC concentration probably vary between different regions, and between lakes of different size, but the described combination of regulatory mechanisms can explain the observed changes in lake productivity along a DOC gradient.

AUTHOR CONTRIBUTIONS

Conceptualisation: JH, EP, SE; Data analysis: JH; Conducting the research, writing: all authors.

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DATA AVAILABILITY STATEMENT

Data are available from the authors upon reasonable request.

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