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Effects of fetch and dissolved organic carbon on epilimnion depth and light climate in small forest lakes in southern Sweden

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Abstract

We sampled small (0.03 to 3.3 km² surface area) forest lakes in southern Sweden during two summers to investigate how concentration of dissolved organic carbon (DOC) and lake size influence epilimnion depth (z_e) and light conditions in the epilimnion. z_e increased with increasing fetch (square root of lake area) but did not decrease with increasing DOC concentration. This suggests greater importance of wind mixing in our study area than in areas with more continental climate, i.e., epilimnion-deepening wind mixing overrides the tendency for epilimnion depth to decrease with increasing DOC concentration. Extinction of photosynthetically active radiation was mainly caused by DOC. The euphotic zone was shallower in the first year than in the second, probably because of higher precipitation and lower solar irradiance in 2007, which together led to higher water color. Mean epilimnetic irradiance was low, especially in 2007, mainly because the increase in DOC did not lead to shallower epilimnia. Browning of lakes in southern Sweden, in combination with a predicted increase in the number of storm events, may lead to more severe light limitation of phytoplankton in small, nutrient-poor lakes, since it may not be accompanied by a compensatory shallowing of the epilimnion. As a consequence, lake ecosystems will become more heterotrophic, CO_2-evasion to the atmosphere will increase, and fish production decrease.

Currently, a great number of northern temperate lakes undergo a browning or "brownification," i.e., increasing water color (Forsberg and Peterson 1990; Evans et al. 2006; Vuorenmaa et al. 2006). Water color is generally tightly related to dissolved organic carbon (DOC) (Pace and Cole 2002), which is in large part comprised of terrestrially derived dissolved humic matter (DHM) that can be yellow to brown in color and thus cause the browning of the water. Several reasons for increasing DOC in lakes have been suggested: Global warming may lead to increased terrestrial and wetland production and increased enzymatic activity in the soils and thus to production of more DOC that can be transported into aquatic ecosystems (Evans et al. 2006). Increased precipitation (Hongve et al. 2004) or changes in seasonal precipitation patterns (Kortelainen 1993) can also lead to increased transport of terrestrial DOC into lakes by mobilizing DOC from different soil layers. The only factor that was related to increasing lake DOC on a large regional scale was decreasing sulfur deposition (Monteith et al. 2007; Erlandsson et al. 2008). As a consequence of increasing pH and decreasing sulfate in soils recovering from acidification, DOC bound in the soils under lower pH is released to soil and groundwater.

Terrestrial DOC strongly absorbs solar radiation of all wavelengths (Kirk 1994; Lean 1998), including the photosynthetically active radiation (PAR), and thus competes with photosynthetic pigments for absorption of photons in the PAR range. Therefore, the euphotic zone (z_{eu}, often roughly defined as the depth where 1% of the surface irradiance remains, but *see* Steemann Nielsen and Hansen 1961; Siegel et al. 2002) becomes shallower with increasing DOC concentration. If the epilimnion is deeper than the euphotic zone, phytoplankton will spend part of their life in an environment where respiration exceeds photosynthesis and if it is deep enough, the net phytoplankton growth is negative. However, many lakes in a continental climate stratify soon after ice-out, forming an epilimnion shallow enough to offer suitable light conditions that allow net positive phytoplankton growth and even bloom formation if the nutrient supply is adequate (Sommer et al. 1986; Huisman and Weissing 1999). In this case, nutrient supply is generally thought to be the limiting factor for phytoplankton growth. However, it has recently been shown that light limitation of both primary and total ecosystem production is strong in humic lakes, and natural variations in DHM override the effects of natural variations in nitrogen and phosphorous on ecosystem production (Karlsson et al. 2009). Although this has been interpreted as an effect mainly from loss of benthic primary production in humic lakes, phytoplankton production should also be negatively affected by increasing DHM. It is important here to distinguish between volumetric and area-integrated production. If phytoplankton production occurs in a thinner water layer in brown-colored lakes, due to a shallowing of the epilimnion, maximal production per volume may not change dramatically, but move closer to the surface. However, area-integrated phytoplankton production will decrease, because an increasing proportion of PAR is absorbed by DOC, not by photosynthetic pigments.

Increasing concentrations of DOC have been shown to lead to decreasing epilimnion depth (z_e) in small (< 5 km² surface area), wind-sheltered forest lakes (Salonen et al. 1984; Fee et al. 1996; Snucins and Gunn 2000). This was explained by the strong light-absorbtion, i.e., solar radiation is absorbed and transformed into heat in a thinner layer of water with increasing DOC concentration. Reduced direct warming at greater depths with increasing DOC should then lead to the formation of a shallow

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epilimnion. However, z_e is also influenced by other factors, and especially in larger lakes wind mixing is an important variable. The potential wind-mixing effect on a lake is often expressed as fetch, the distance wind can blow over a lake uninterrupted by obstacles. Fetch is influenced by predominant wind directions, the shape of the basin, and the surroundings. Wind will have a stronger mixing effect the higher the wind speed, the longer the duration of strong winds, and the longer the fetch. If a small lake lies in a deep depression or is surrounded by high trees, wind has a smaller mixing potential than if the same lake is situated in a flat, treeless area. For lakes in a limited geographical area wind directions and wind speed are approximately the same for all lakes. Disregarding variations in the surrounding terrain, the important variable is then fetch, which is often simplified to the square root of the lake area. Gorham and Boyce (1989), Fee et al. (1996), and King et al. (1997) have shown that z_e increases with increasing fetch (lake size or area).

Depending on how DOC influences z_{eu} and z_e in lakes, there are different possible scenarios for the phytoplankton community in lakes that experience increasing DOC: If z_{eu} and z_e are both influenced to the same extent by increasing DOC, then the decrease in z_e will to some extent be able to compensate for the decrease in z_{eu}. In that case, phytoplankton will not experience decreasing mean light intensities in the epilimnion (although phytoplankton will be restricted to a thinner layer, decreasing production per unit area). However, if the decrease in z_e is not able to compensate for decreasing z_{eu}, the epilimnion could become deeper than the euphotic zone and phytoplankton growth would then be negative in a part of the epilimnion (Houser 2006). Since increasing wind-mixing leads to a deeper epilimnion, phytoplankton in large lakes are expected to be more light limited than phytoplankton in small lakes with similar water color (Jones et al. 1996). As climate change may lead to more extreme weather conditions, including stronger winds and an increasing number of storm events (IPCC 2007), a deepening of the epilimnion may be one consequence, and this could contribute to a further mean darkening of this habitat, in addition to the effect from brownification. These changes are expected to have a significant effect on the phytoplankton community, including species composition, growth rates, and productivity (Jones et al.1996; Diehl et al. 2002). Essentially, this is the classical question of the influence of the ratio between mixed layer and photic zone depth on phytoplankton photosynthesis (Sverdrup 1953; Riley 1957; Siegel et al. 2002) developed for marine conditions, but also relevant for lakes (Huisman and Weissing 1999; Houser 2006; Loiselle et al. 2007).

Our aim was to investigate how variables describing lake morphometry (lake maximum depth, lake area, fetch) and water color (Secchi depth, water color [colorimetrically], DOC concentration, absorbance at 440 nm) influence epilimnion depth and light availability for phytoplankton during summer. We determined epilimnion depth and light conditions during the summers of two consecutive years in southern Swedish forest lakes (38 lakes in 2007 and 20 lakes in 2008). The DOC concentration in the lakes ranged widely (3.7 to 26.9 mg L^{-1} in 2007) and represented the typical variation for lakes in this area. We expected that increasing DOC concentrations would lead to decreasing epilimnion depth (z_e) in our lakes, while fetch would play a minor role in determining z_e, since all studied lakes were small (< 5 km^2 area). Water color was also expected to be the main factor controlling both the mean epilimnetic irradiance $\bar{E}\%$ and euphotic depth, z_{eu}. However, we expected z_{eu} to change more with increasing DOC than z_e (Houser 2006), leading to higher $z_e : z_{eu}$ ratios and lower $\bar{E}\%$ with increasing DOC. Thus, we expected mean PAR intensities in the epilimnia to be lowest in lakes that are both large and brown, leading to the most adverse conditions for phytoplankton growth in these lakes.

Methods

Study area—All study lakes are situated within an approximately 100-km distance of the limnological field station at Aneboda (Einar Naumann Laboratory, 57°07′N, 14°34′E) where the landscape is dominated by coniferous forest. Thirty-eight lakes were sampled between 02 and 27 July 2007. From these lakes, 20 that had stratified during 2007 were chosen and sampled again between 30 June and 07 July 2008. Physical conditions in the lakes change only modestly at this time of the year and vertical temperature stratification is thus stable (data not shown).

Sampling—Each lake was visited once during each year and sampling was conducted from a boat at the deepest part of the lake. Secchi depth was measured using a 20-cm-diameter white disk. A 2-m plexiglas tube was used to obtain subsamples containing an equal volume of water from all depths within the epilimnion, i.e., 0–2 m and 2–4 m, etc. (or 0–1 m and 1–3 m, etc. when epilimnion depth was uneven). All subsamples were mixed to represent a complete, integrated water sample from the epilimnion. Since bathymetric maps were only available for some of the lakes, water samples were thus not volume weighted. Profiles of temperature and PAR were measured in 0.1-m increments using a multiprobe (Alec AAQ1183).

Lake morphology and water chemistry—Concentrations of total nitrogen (TN) and total phosphorous (TP) were measured on integrated epilimnion water following standard methods (Schimadzu 6500 TOC-analyzer for TN; IPC MS ELAN-6000 for TP). Samples were stored frozen in acid-washed polyethylene bottles before analysis. Concentrations of TP in 2007 ranged from 3.2 to 22.4 μg L^{-1} (mean 8 μg L^{-1}), covering a range from ultraoligo- to mesotrophic lakes (Wetzel 2001), but with the average lake being oligotrophic.

DOC concentration was measured on integrated epilimnion water that was filtered through precombusted GF/F filters (4 h, 550°C) and stored frozen in acid-washed polyethylene bottles. The samples were acidified with 2 mol L^{-1} HCl to pH < 2 and analyzed after sparging with CO_2-free air using a Schimadzu 5000 TOC analyzer. Water color was measured in two ways using integrated epilimnion water filtered through a GF/F filter: colorometrically using a Hellige Aqua Tester (the platinum scale), and as absorbance at 440 nm using a Beckman Coulter DU800 spectrophotometer with a 1-cm cuvette, which is a measure of how strong radiation is absorbed by the humic fraction of the DOC. For analysis of chlorophyll *a* (Chl *a*) concentrations, integrated epilimnion water was prescreened through a 150-μm nylon net before filtration onto a GF/F filter that was stored frozen before analysis (Marker et al. 1980).

Data on lake areas were provided by the county boards of Jönköping and Kronoberg. Fetch was calculated as the square root of lake area. Morphometric characteristics and water chemistry of the study lakes are presented in Tables 1 and 2.

Epilimnion depth—Epilimnion depth (z_e) was obtained graphically as the intersection of two trend lines, one through the upper part of the epilimnion and one through the metalimnion (Wetzel 2001). In three of the lakes sampled in 2007 and in one lake in 2008, it was not possible to define z_e since temperature changed either gradually or was stable throughout the water column. The final data sets consist therefore of 35 lakes in 2007 and 19 lakes in 2008.

Light conditions—The means of the PAR values recorded at the surface were 446.7 μmol m^{-2} s^{-1} in 2007 and 515.5 μmol m^{-2} s^{-1} in 2008 (range from 50.4 to 1725.4 μmol m^{-2} s^{-1} in 2007 and from 24.4 to 1177.0 μmol m^{-2} s^{-1} in 2008). Mean epilimnetic irradiance as a proportion of surface irradiance was calculated using the equation introduced by Sterner (1990),

$$\bar{E}\,\% = \frac{100 \times (1 - e^{-kz_e})}{kz_e} \qquad (1)$$

where $\bar{E}\,\%$ is the mean epilimnetic irradiance (uncorrected for lake morphology) in percentage of the surface radiation, k is the attenuation coefficient of PAR, and z_e is the epilimnion depth as obtained above. k was calculated as the slope of a linear regression of the log-transformed PAR values against depth in the water column. Only data lying on a straight line were included in the linear regressions (R^2 values ranged from 0.9142 to 0.9973, mean 0.9857 in 2007 and from 0.9391 to 0.9991, mean 0.9842 in 2008). The same linear regression was used to calculate the euphotic depth (z_{eu}), i.e., the depth where 1% of the incoming solar radiation just above the water surface was left.

Statistical analysis—SPSS (Statistical Package for the Social Sciences) version 14.0 was used for all statistical analysis. Pearson correlation analysis was used to identify which of the included variables (lake maximum depth, lake area, fetch, water color, DOC concentration, absorbance at 440 nm, Secchi depth, Chl *a*) were significantly related to epilimnion depth and mean epilimnetic irradiance. Data were log-transformed before analysis if necessary to meet assumptions for the tests. We also performed partial correlation analyses to correct for possible relations between the factors. For z_e we included lake maximum depth, fetch, DOC, and Chl *a* in the analysis and for $\bar{E}\,\%$ we included fetch, DOC, Chl *a*, and z_e. These parameters were chosen to represent important potential influences on z_e and $\bar{E}\,\%$, respectively, while avoiding autocorrelations between included variables as far as possible. Both Pearson and partial correlation analyses were performed for each year separately to enable intercomparisons.

Results

Water chemistry—Most lakes had DOC concentrations between 5 and 15 mg L^{-1} (Tables 1, 2). DOC concentration was closely and linearly related to water color and absorbance at 440 nm in our data and was included in the partial correlation analysis as the variable representing water color to achieve comparability with other studies. DOC and fetch were not related to each other in this data set (Spearman's rank test, 2007: $R = 0.31$, $p = 0.858$; 2008: $R = 0.232$, $p = 0.339$; Fig. 1).

Epilimnion depth—Epilimnion depth ranged from 1.5 to 7.0 m (mean 4.1 m) in 2007 (Table 1) and from 1.7 to 6.5 m (mean 3.4 m) in 2008 (Table 2). Among the tested variables (lake maximum depth, lake area, fetch, water color, DOC concentration, absorbance at 440 nm, Secchi depth, Chl *a* concentration), only lake maximum depth, fetch (Fig. 2), and lake area were significantly correlated to z_e (Table 3). All relationships are positive correlations, i.e., z_e increases with increasing lake depth, fetch, and area. There was also a positive significant correlation between z_e and Secchi depth in 2008 ($R = 0.554$, $p = 0.014$). This relation was, however, significant because of one outlier and disappeared when this lake was excluded ($R = 0.187$, $p = 0.456$). Thus, none of the parameters related to water color had a significant effect on z_e and z_e did not decrease with increasing DOC concentration (Fig. 3), implying that wind mixing is the most important factor determining z_e in these lakes.

Since we did not expect that only variables representing lake morphometry influence z_e, we performed a partial correlation analysis to correct for effects of potential relations between variables. We included lake maximum depth, fetch, DOC concentration, and Chl *a* concentration. However, the partial correlation analysis did not reveal any new significant relations; fetch was the only parameter significantly related to z_e in both 2007 and 2008 (Table 4). Neither DOC nor Chl *a* concentration gained in importance, and lake maximum depth lost its significant correlation with z_e (Table 4), again implying that fetch, a variable representing wind mixing, is the only important factor related to z_e in our data set.

Mean epilimnetic irradiance—Mean epilimnetic irradiance ranged from 12.4% to 73.4% (mean 39.6%) of the surface radiation in 2007 (Table 1) and from 22.5% to 80.0% (mean 48.2%) in 2008 (Table 2). In the 19 lakes that were sampled in both years $\bar{E}\,\%$ was higher in 2008 than in 2007 in 13 lakes, and there was a significant difference between $\bar{E}\,\%$ in the two study years (paired samples *t*-test, $t = -2.439$, df = 18, $p = 0.025$).

Table 1. Lake morphology and water chemistry for 35 southern Swedish lakes sampled during July 2007.

Lake name	Depth (m)	Area (km^2)	Fetch (m)	DOC (mg L^{-1})	Absorbance (cm^{-1})	Water color (mg Pt L^{-1})	Secchi depth (m)	Chl *a* (μg L^{-1})	Residence time (yr^{-1})	z_e (m)	z_{eu} (m)	$z_e : z_{eu}$ ratio	$\bar{E}$ %
Hojagöl	15.7	0.03	173.2	6.92	0.023	15	2.71	6.4	-	1.5	4.2	4.26	73.4
Källshultasjön	9.7	0.20	447.2	8.26	0.027	30	1.76	6.9	1.9	5.6	3.6	1.24	26.4
Burken	6.7	0.20	447.2	11.03	0.027	70	2.09	5.9	1	2.8	3.7	2.10	49.4
Hultasjön	12.0	0.20	447.2	11.71	0.035	40	1.95	4.4	0.4	2.2	3.4	1.98	54.3
Älgarydsjön	7.0	0.20	447.2	11.77	0.044	200	1.21	5.1	0.3	3.1	2.1	1.66	28.1
Fersjön	9.8	0.20	447.2	18.01	0.064	100	0.99	5.9	1.9	1.7	2.2	3.47	38.9
Skirsjön	9.6	0.30	547.7	6.20	0.012	0	3.43	3.2	3.5	3.4	7.7	0.94	61.0
Hacksjön	7.1	0.30	547.7	7.90	0.021	40	1.89	33.7	1.42	2.7	4.4	12.49	54.7
Hisshultasjön	7.8	0.30	547.7	8.75	0.017	40	2.18	8.9	0.3	2.6	3.1	3.42	55.9
Boasjön	12.9	0.30	547.7	8.96	0.036	60	1.72	5.6	2.1	3.7	2.5	1.50	30.9
Gyslättasjön	9.2	0.30	547.7	12.24	0.037	60	1.45	7.3	1	2.4	1.9	3.03	40.2
Kolvesjön	15.3	0.30	547.7	12.33	0.034	40	1.67	3.3	0.3	4.6	4.7	0.72	51.9
Svanåsasjön	10.0	0.30	547.7	17.67	0.050	100	1.25	6.2	0.3	2.2	5.3	2.80	43.2
Hagesjön	8.9	0.30	547.7	20.80	0.073	120	0.94	8.3	0.7	2.4	1.8	3.47	33.1
Feresjön	13.3	0.40	632.5	5.85	0.018	5	2.98	4.7	0.3	3.2	5.1	1.46	58.1
Hagserydssjön	10.2	0.40	632.5	21.06	0.060	100	1.13	4.6	-	2	2.0	2.32	38.3
Åbodasjön	8.0	0.50	707.1	10.99	0.027	40	1.62	7.7	0.5	3.8	2.6	2.02	37.0
Hökasjön	10.8	0.60	774.6	9.47	0.029	30	2.35	5.9	0.7	3.5	4.1	1.70	47.3
Holmeshultasjön	16.5	0.70	836.7	9.07	0.023	20	2.33	6.0	2	4.4	4.2	1.37	41.3
Idesjön	14.5	0.70	836.7	13.49	0.033	30	2.03	5.1	0.4	6.2	3.9	0.82	26.9
Hemmesjösjön	5.8	0.70	836.7	13.80	0.042	60	1.24	16.9	0.8	4.3	2.3	3.94	25.5
Teresjön	34.0	0.80	894.4	6.79	0.019	20	2.49	4.3	2.3	4.4	5.3	0.97	43.3
Djupasjön	20.2	0.80	894.4	14.40	0.031	40	2.36	4.2	1	5.4	3.9	0.78	31.3
Holmasjön	14.2	0.90	948.7	7.05	0.014	0	3.75	5.0	3.5	6.2	5.8	0.81	42.7
Klintsjön	16.7	1.00	1000.0	3.70	0.006	10	4.00	4.1	2.2	3.8	10.2	1.07	61.1
Förhultasjön	6.7	1.00	1000.0	9.90	0.021	40	2.43	4.5	0.82	4.2	3.5	1.07	44.5
Juven	9.6	1.00	1000.0	20.36	0.073	100	0.88	10.8	0.73	5.9	1.2	1.83	12.4
Åredasjön	9.0	1.20	1095.4	10.84	0.030	40	1.60	18.0	2	5.9	2.7	3.05	21.7
Boskvarnasjön	19.7	1.20	1095.4	17.02	0.057	100	1.13	10.8	0.5	7	2.7	1.54	13.4
Yasjön	16.3	1.30	1140.2	10.16	0.029	40	1.98	4.5	0.6	4.3	2.6	1.05	36.6
Madsjön	8.6	1.30	1140.2	13.34	0.035	20	1.60	8.3	2.1	5	3.6	1.66	30.4
Kinnen	15.0	1.40	1183.2	22.81	0.052	100	1.47	6.0	1.2	5.5	2.0	1.09	19.8
Fiolen	9.0	1.50	1224.7	6.37	0.012	5	2.93	7.3	3.9	5.3	5.2	1.38	46.4
Linnerydssjön	6.7	1.50	1224.7	26.85	0.081	140	0.75	28.5	0.3	4.2	1.6	6.78	13.3
Skärlen	25.0	3.30	1816.6	3.88	0.007	0	5.36	2.6	8.4	6.2	12.9	0.42	54.8

Pt, platinum (Hazen units).

Table 2. Lake morphology and water chemistry for 19 southern Swedish lakes sampled during June and July 2008.

Lake name	Depth (m)	Area (km²)	Fetch (m)	DOC (mg L^{-1})	Absorbance (cm^{-1})	Water color (mg Pt L^{-1})	Secchi depth (m)	Chl *a* (μg L^{-1})	Residence time (yr^{-1})	z_e (m)	z_{eu} (m)	$z_e : z_{eu}$ ratio	$\bar{E}$ %
Hojagöl	15.7	0.03	173.2	5.77	0.015	40	2.63	3.4	-	2.2	4.3	0.51	64.6
Burken	6.7	0.20	447.2	11.95	0.029	80	1.85	4.7	1	3.1	4.3	0.72	42.1
Hultasjön	12.0	0.20	447.2	10.68	0.024	80	2.35	3.2	0.4	1.8	5.4	0.34	71.0
Skirsjön	9.6	0.30	547.7	5.98	0.008	20	3.63	3.3	3.5	3.9	7.8	0.50	59.4
Hisshultasjön	7.8	0.30	547.7	10.14	0.020	60	2.11	7.2	0.3	3.5	4.6	0.77	50.1
Gyslättasjön	9.2	0.30	547.7	11.18	0.027	80	1.65	3.6	0.3	1.7	4.2	0.40	59.4
Kolvesjön	15.3	0.30	547.7	8.79	0.018	50	2.60	2.0	0.3	2.3	5.8	0.39	63.8
Svanåsasjön	10.0	0.30	547.7	14.62	0.043	100	1.40	6.4	1	3.4	2.9	1.16	49.3
Hagesjön	8.9	0.30	547.7	19.28	0.067	240	0.95	16.9	0.7	1.8	1.6	1.17	40.5
Feresjön	13.3	0.40	632.5	6.18	0.010	30	3.08	2.3	0.3	3.8	7.4	0.51	53.4
Hagserydssjön	10.2	0.40	632.5	20.62	0.060	160	0.95	11.7	-	1.8	2.8	0.66	44.9
Hökasjön	10.8	0.60	774.6	10.30	0.022	70	2.35	4.3	0.7	3.1	5.7	0.54	51.5
Holmeshultasjön	16.5	0.70	836.7	9.83	0.020	50	2.78	3.6	2	4.1	5.8	0.71	42.5
Idesjön	14.5	0.70	836.7	14.35	0.032	80	2.13	3.4	0.4	4.1	2.3	1.75	37.8
Djupasjön	20.2	0.80	894.4	17.88	0.036	100	1.88	3.3	1	4.0	4.6	0.87	35.6
Boskvarnasjön	19.7	1.20	1095.4	16.09	0.050	120	1.40	5.5	0.5	5.6	3.0	1.83	22.5
Yasjön	16.3	1.30	1140.2	11.53	0.029	80	2.28	3.0	0.6	4.8	5.5	0.88	36.3
Kinnen	15.0	1.40	1183.2	20.62	0.061	200	1.25	4.7	1.2	3.8	3.4	1.13	30.5
Skärlen	25.0	3.30	1816.6	4.20	0.004	10	6.60	1.2	8.4	6.5	13.8	0.47	58.2

Pt, platinum (Hazen units).

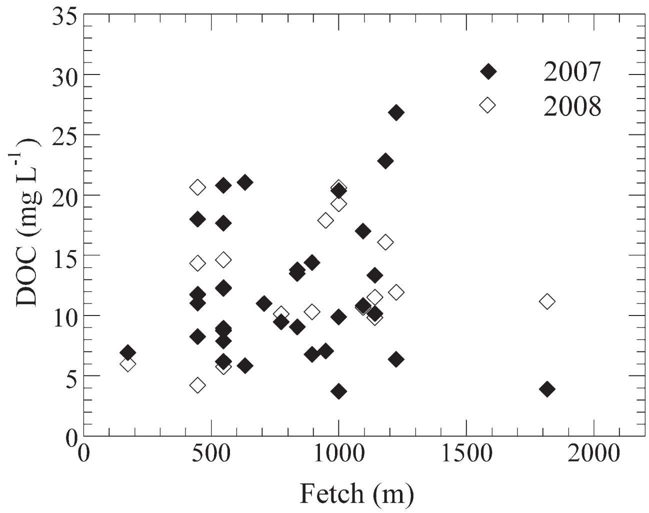

Fig. 1. DOC concentration vs. fetch for 35 southern Swedish lakes in 2007 ($R = 0.31$, $p = 0.858$) and 19 lakes in 2008 ($R = 0.232$, $p = 0.339$).

In 2007, the highest values for $\bar{E}$ % were in low-DOC lakes independent of lake size, whereas the lowest values were in lakes with high DOC and a size of at least 1 km². This conclusion cannot be drawn from the 2008 data since too few lakes with an area > 1 km² were included. As expected, $\bar{E}$ % was strongly related to variables representing water color and to Chl *a* concentrations (Fig. 4, Table 5). $\bar{E}$ % was correlated to both z_e and fetch in 2007, but not in 2008 (Fig. 5). Since $\bar{E}$ % was calculated using z_e, a strong correlation between the two variables was expected. The lack of this relationship in 2008 may be because too few lakes were included in the data set. To test this, we performed the correlation analysis for the whole data set. No changes of general relations appeared, but relationships between $\bar{E}$ % and both z_e ($R = -0.525$, $p = 0.000$) and fetch ($R = -0.362$, $p = 0.007$) were strengthened.

Partial correlation analysis was performed to investigate the influence of different variables on $\bar{E}$ % when correcting for the influence of other factors. We included DOC, Chl *a* concentration, fetch, and z_e in the analysis (Table 6). Strong correlations were obtained for both DOC and z_e, which was expected since $\bar{E}$ % was calculated using z_e and the attenuation coefficient k, which is highly influenced by DOC. Thus, the overall light conditions in the epilimnion depend on both the depth of the epilimnion and the DOC concentration. For 2007, there was also a negative correlation between $\bar{E}$ % and Chl *a* concentration, though rather weak. The only factor without any significant relation to $\bar{E}$ % in the partial correlation analysis was fetch. This was also the case when performing the partial correlation analysis for both years together ($R = 0.090$, $p = 0.530$), and when additionally excluding the outlier from the analysis ($R = -0.007$, $p = 0.962$).

Euphotic depth—Euphotic depth ranged from 1.2 m to 12.9 m (mean 4.0 m) in 2007 and the ratio of z_e to z_{eu} ranged from 0.4 to 5.0 (mean 1.3). The ratio is > 1 in 21

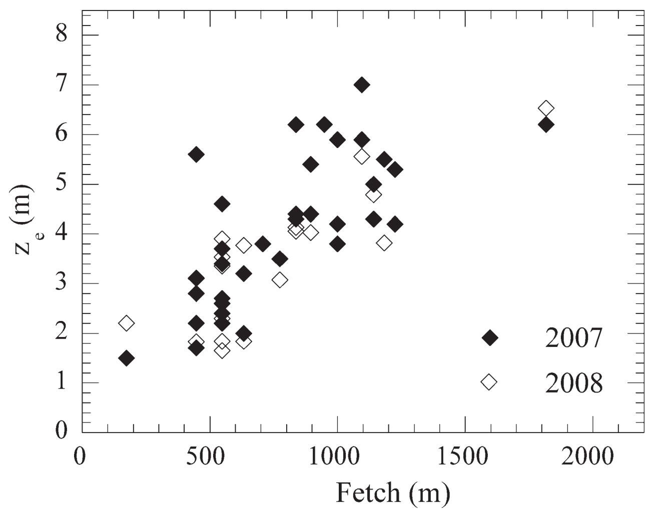

Fig. 2. Epilimnion depth z_e vs. fetch for 35 southern Swedish lakes in 2007 ($R = 0.721$, $p = 0.000$) and 19 lakes in 2008 ($R = 0.822$, $p = 0.000$).

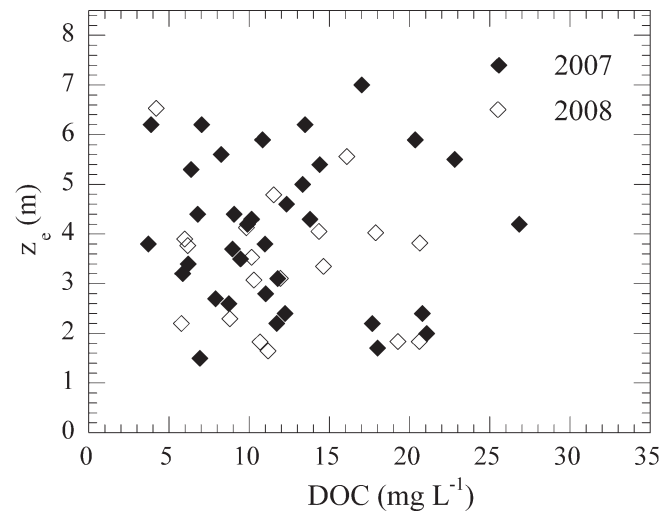

Fig. 3. Epilimnion depth z_e vs. DOC concentration for 35 southern Swedish lakes in 2007 ($R = -0.033$, $p = 0.851$) and 19 lakes in 2008 ($R = -0.201$, $p = 0.409$).

lakes, i.e., the epilimnion was deeper than the euphotic zone in more than half of our lakes in 2007. In 2008, z_{eu} was generally deeper than in 2007 and ranged from 1.6 to 13.9 m (mean 5.0 m). The difference between z_{eu} for the 2 yr is significant (paired samples *t*-test, $t = -2.822$, df = 18, $p = 0.011$), and z_{eu} was deeper in 2008 than in 2007 in 16 of the 19 lakes that were sampled twice. Deeper z_{eu} led to lower $z_e : z_{eu}$ ratios (range from 0.3 to 1.8, mean 0.8) and the ratio was > 1 in only 5 lakes, whereas 10 of these 19 lakes had a ratio > 1 in 2007.

Since the study was conducted during summer, when stratification was stable, the values of the $z_e : z_{eu}$ ratios presented here are probably yearly maxima, undoubtedly being well above 1 for some of the studied lakes during other periods of the year. When lakes are unstratified in spring and autumn the $z_e : z_{eu}$ ratio can be expected to be highly unfavorable for phytoplankton growth in brown-colored lakes.

Discussion

As expected, mean epilimnetic irradiance decreased in both study years with increasing DOC concentration and epilimnion depth (z_e). However, contrary to our expectations, z_e did not decrease with increasing DOC, but did increase with increasing fetch. This means that a shallower euphotic zone due to increasing DOC concentration was not accompanied by a shallowing of the epilimnion.

Epilimnion depth—In both years, z_e was only influenced by lake morphometry, especially fetch (Fig. 2). This is contrary to results from other studies (Pérez-Fuentetaja et al. 1999; Snucins and Gunn 2000) where z_e depended on DOC in small lakes (< 5 km^2 surface area), whereas fetch influenced z_e only in larger lakes (> 5 km^2; Fee et al. 1996). We therefore expected variables related to the brownness of the water, i.e., DOC concentration, water color, absorbance at 440 nm, and Secchi depth, to affect z_e. This was not found in our data set (Fig. 3), even when correcting for the influence of other potentially important factors (lake maximum depth, fetch, and Chl a concentrations) in a partial correlation analysis. The relation between lake maximum depth and z_e has been studied earlier (Gorham and Boyce 1989). Yet, there was only a significant correlation in the Pearson correlation analysis but not in the partial correlation analysis. This implies that the

Table 3. Pearson correlation coefficients (R) and p-values for relationships between a number of variables and epilimnion depth z_e in July 2007 and July 2008. The values in parentheses for Secchi depth in 2008 denote the correlation excluding one outlier.

Variable	R (2007)	P	R (2008)	p
Depth (m)	0.345	0.043*	0.693	0.001**
Area (km^2)	0.646	0.000***	0.794	0.000***
Fetch (m)	0.721	0.000***	0.822	0.000***
Water color (mg Pt L^{-1})	−0.214	0.217	−0.311	0.195
DOC (mg L^{-1})	−0.033	0.851	−0.201	0.409
Absorbance (cm^{-1})	−0.121	0.496	−0.245	0.313
Secchi depth (m)	0.207	0.233	0.554 (0.187)	0.014* (0.456)
Chlorophyll *a* (μg L^{-1})	0.005	0.977	−0.416	0.076

Pt, platinum (Hazen units).
* $p < 0.5$; **$p < 0.01$; ***$p < 0.001$.

Table 4. Results of the partial correlation analysis for epilimnion depth z_e in July 2007 and July 2008.

Variable	R (2007)	p	R (2008)	p
Depth (m)	0.119	0.516	0.094	0.73
Fetch (m)	0.674	0.000***	0.699	0.003**
DOC (mg L^{-1})	−0.039	0.832	−0.247	0.356
Chlorophyll *a* (μg L^{-1})	−0.007	0.969	−0.104	0.701

** $p < 0.01$; ***$p < 0.001$.

Table 5. Pearson correlation coefficients (R) and p-values for relationships between a number of variables and mean epilimnetic irradiance $\bar{E}\%$ in July 2007 and in July 2008. Some of the data (water color, DOC concentration, absorbance, Secchi depth, and Chl *a* concentration) were $\log_{10}$-transformed before the statistical analysis.

Variable	R (2007)	p	R (2008)	p
Depth (m)	0.131	0.452	−0.195	0.424
Area (km^2)	−0.217	0.21	−0.240	0.323
Fetch (m)	−0.335	0.049*	−0.415	0.077
Water color (mg Pt L^{-1})	−0.549	0.001**	−0.560	0.013*
DOC (mg L^{-1})	−0.697	0.000***	−0.672	0.002*
Absorbance (cm^{-1})	−0.675	0.000***	−0.641	0.003**
Secchi depth (m)	0.685	0.000***	0.500	0.029*
Chlorophyll *a* (μg L^{-1})	−0.433	0.009**	−0.386	0.102
Epilimnion depth (m)	−0.523	0.001**	−0.438	0.060

Pt, platinum (Hazen units).
* $p < 0.5$; **$p < 0.01$; ***$p < 0.001$.

relation may be an effect of the strong relation between lake size, and thus fetch, and lake depth.

That fetch was the only factor influencing z_e in the partial correlation analysis was unexpected, since the effect on epilimnion depth of wind mixing was thought to be limited in the relatively small lakes (lake area < 5 km^2) in our study. Sterner (1990) found a relationship between fetch and z_e similar to the one presented here in lakes covering a large size range (approximately 0.02 to 20 km^2) in Ontario, Canada. However, these lakes were described as being "colorless," whereas DOC had a large range and high maximum values in our lakes. Additionally, other studies did not find fetch to be a good predictor of z_e in lakes with a surface area up to10 km^2 (Zimmerman et al. 1983; Mazumder et al. 1990), which is larger than for the lakes we investigated. Mazumder et al. (1990) showed that z_e increased with increasing water clarity (increasing Secchi depth). Other studies found that z_e decreases with increasing DOC in lakes with similar sizes (< 5 km^2) but lower maximum values in DOC than our lakes (Pérez-Fuentetaja et al. (1999): 12.41 mg DOC L^{-1}; Keller et al. (2006): 5.2 mg DOC L^{-1}; Snucins and Gunn (2000): 17.4 mg DOC L^{-1}). We therefore expected that increasing DOC concentrations would counteract the deepening of the epilimnion with increasing fetch and thus override or at least weaken the relation between fetch and z_e. This was, however, not the case. Under the assumption that there is a minimum lake size below which a lake is no longer influenced by wind mixing, i.e., changing DOC can influence z_e, this implies that this critical lake size is smaller in our study lakes than other studies have found (Fee et al. 1996; Pérez-Fuentetaja et al. 1999; Snucins and Gunn 2000).

Weather conditions during the two study years were markedly different for both spring and summer (Table 7), yet relations of fetch and DOC to mixed-layer depth were similar in both years. Thus an influence of anomalous weather on our results seems unlikely. Differences between years were moderate during April, which in 2007 was dryer and warmer with higher solar irradiance than April 2008, but both years were dryer, warmer, and had higher solar irradiance than mean values for 1961–1990. A striking difference was in precipitation during May, with values

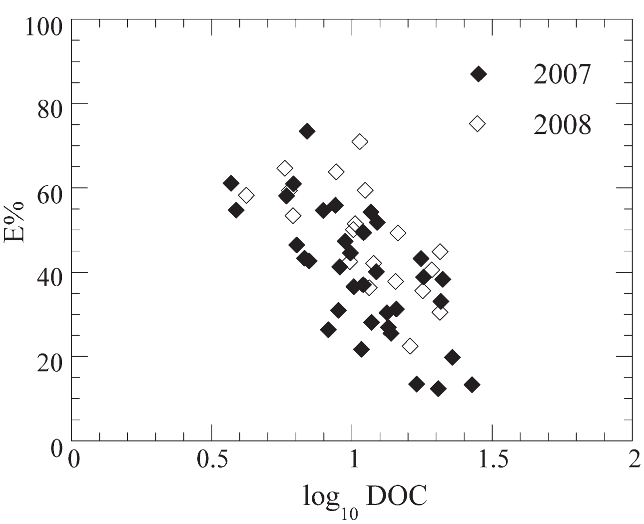

Fig. 4. Mean epilimnetic irradiance $\bar{E}\%$ as a proportion of surface irradiance vs. $\log_{10}$-transformed DOC concentrations for 35 southern Swedish lakes in 2007 ($R = -0.697$, $p = 0.000$) and 19 lakes in 2008 ($R = -0.672$, $p = 0.002$).

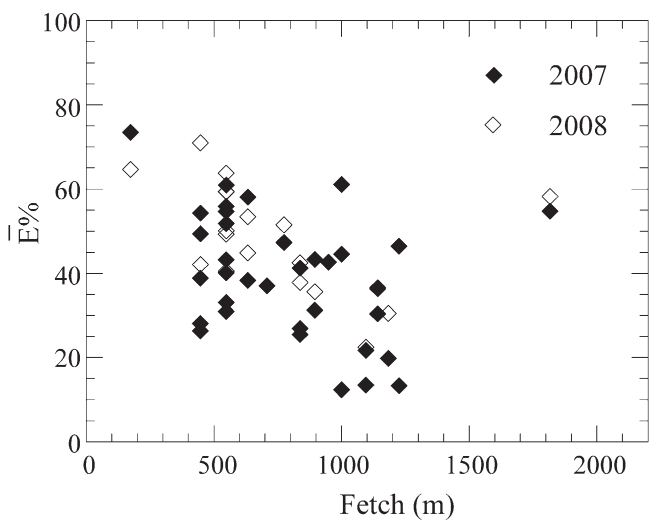

Fig. 5. Mean epilimnetic irradiance $\bar{E}\%$ as a proportion of surface irradiance vs. fetch for 35 southern Swedish lakes in 2007 ($R = -0.335$, $p = 0.049$) and 19 lakes in 2008 ($R = -0.415$, $p = 0.077$).

Table 6. Results of the partial correlation analysis for mean epilimnetic irradiance $\bar{E}$ % as a proportion of surface irradiance in July 2007 and July 2008; data for DOC and Chl *a* concentration were $\log_{10}$-transformed before the statistical analysis.

Variable	*R* (2007)	*p*	*R* (2008)	*p*
Fetch (m)	0.033	0.858	0.298	0.262
DOC (mg L^{-1})	−0.827	0.000***	−0.819	0.000***
Chlorophyll *a* (μg L^{-1})	−0.353	0.047*	−0.254	0.343
Epilimnion depth (m)	−0.692	0.000***	−0.803	0.000***

* $p < 0.5$; ***$p < 0.001$.

above the mean in 2007, whereas in 2008 precipitation was only half of the mean value for 1961–1990. In both years temperatures in May were above the mean, but 2008 was warmer and had higher solar irradiance than May 2007. During June, the difference in precipitation was even stronger than for May, above the mean in 2007 but below in 2008. Temperature was higher in 2007 than in 2008, whereas June 2008 had higher solar irradiance than June 2007. The difference in precipitation during July was large; it was above the mean value in both years, but more than double in 2007 than 2008. Temperature and solar irradiance for July were lower in 2007 than in 2008. However, sampling in 2008 was done during a short period in the beginning of July. Thus weather conditions in July 2008 probably had little influence on stratification when the lakes were sampled, whereas for 2007 sampling included a substantial part of July. In conclusion, weather conditions differed markedly between the two study years, and yet relationships between z_e, fetch, DOC, and water color were the same.

Regional climatic differences may explain the different effects of DOC and fetch on z_e in our study compared with what has been reported by others. Earlier studies on DOC, fetch, and z_e were in Canada (Fee et al. 1996; Pérez-Fuentetaja et al. 1999; Snucins and Gunn 2000) and Finland (Salonen et al. 1984), where climate is more continental than in southern Sweden, which has a considerably stronger maritime influence. In a continental climate, lakes warm more rapidly after ice-out than in a more maritime climate, so that a stable lake stratification is established more quickly in a continental climate. In contrast, warming during spring is a comparatively slow process in southern Sweden, so that a larger number of storm events may occur, deepening the epilimnion. The number of storm events during the stratification period is known to affect year-to year-variation of epilimnion depth (Wetzel 2001) and Hutchinson (1957) argues that stratification is less stable in lakes in an oceanic climate. However, there seem to be no comparative studies on regional variations in z_e related to climate.

Light conditions in the epilimnion—For both study years, the mean epilimnetic solar radiation as a percentage of the surface value ($\bar{E}$ %) depended on several factors, including the brownness of the water (water color, DOC concentration, absorbance at 440 nm, and Secchi depth) (Fig. 4), Chl *a* concentrations, as well as z_e and fetch (Fig. 4). This confirms that DOC, or in particular humic matter, is a strong absorber of solar radiation in these rather unproductive lakes (Birge and Juday 1934; Schindler 1971), which can also be seen from the shallow z_{eu}. It also reflects the fact that $\bar{E}$ % is calculated using z_e. The relation with fetch in the Pearson correlation analysis can thus be explained by the relation between fetch and z_e that was discussed earlier. Consequently, light intensity in the epilimnion is not only determined by DOC, but also by the depth of the epilimnion, which itself depends on fetch. Accordingly, the lowest $\bar{E}$ % are found in larger lakes, i.e., lakes with a deeper epilimnion, that additionally have high DOC.

The negative correlation between Chl *a* and $\bar{E}$ % is somewhat counterintuitive, since one would expect phytoplankton biomass to decrease when light intensities decrease. Yet, phytoplankton may be strong absorbers of light themselves and thus increasing Chl *a* concentrations will lead to decreasing $\bar{E}$ %, independent of DOC concentrations. Alternatively, cells may acquire more Chl *a* in a low light environment to be able to harvest more light (Latasa 1995). This hypothesis is supported by our data: Increasing DOC leads to decreasing $\bar{E}$ %, and decreasing $\bar{E}$ % leads to increasing Chl *a*. If this is the case, Chl *a* may not actually reflect phytoplankton biomass, which makes interpretation of these results difficult without additional

Table 7. Weather conditions at the weather station in Växjö within our study area from April to July for the study years 2007 and 2008 compared with mean values for the period 1961–1990; data from the Swedish Meteorological and Hydrological Institute (http://www.smhi.se/cmp/jsp/polopoly.jsp?d=10963&l=sv).

Month	Year	Temperature (°C)	Precipitation (mm)	Solar irradiance (kW h m^{-2})
Apr	Mean	4.7	37	104.9
	2007	8.0	20	142.9
	2008	6.7	25	119.8
May	Mean	10.2	44	146.3
	2007	11.5	57	143.0
	2008	12.1	20	180.7
Jun	Mean	14.3	53	157.4
	2007	16.1	78	158.2
	2008	14.3	37	174.3
Jul	Mean	15.3	72	146.0
	2007	14.9	215	131.5
	2008	17.1	101	177.5

information on phytoplankton communities in the studied lakes. However, since a majority of lakes in southern Sweden are oligotrophic, with TP on the order of 10–20 μg L^{-1} and Chl *a* up to 10 μg L^{-1} (database of the Swedish University of Agricultural Sciences [SLU], http://info1.ma.slu.se/db.html), $\bar{E}\,\%$ is not markedly influenced by phytoplankton pigments. On the other hand the mean DOC concentration for southern Swedish lakes is roughly 15 mg L^{-1} (SLU database), which implies a strong effect on $\bar{E}\,\%$.

There were differences between the years in $\bar{E}\,\%$, z_{eu}, and the $z_e : z_{eu}$ ratio for our lakes. These differences can most likely be explained by less precipitation and more sunshine in 2008 compared with 2007. Whereas higher than average precipitation led to an increased input of refractory colored DOC to the lakes in 2007, higher solar radiation in 2008 led to increased photobleaching of DOC (Granéli et al. 1996). This is supported by data on water chemistry. Although DOC concentrations did not differ significantly between years, absorbance did (Wilcoxon signed ranks test, $z = -2.558$, $p = 0.011$), which implies that DOC was less colored in 2008 than in 2007. Thus, light availability for phytoplankton in the epilimnion was probably higher in 2008 compared with 2007. Still, even in 2008 $\bar{E}\,\%$ was low in most lakes and the $z_e : z_{eu}$ ratio was rather high in some lakes.

Implications for phytoplankton—In this study, z_{eu} was shallow in most lakes, and $\bar{E}\,\%$ as well as $z_e : z_{eu}$-ratios indicate that light intensities in the epilimnion are low, especially in larger lakes with high DOC. How this affects the phytoplankton communities in the lakes is not clear. Houser (2006) found that the decrease in z_e, which was related to increasing DOC concentrations in that study, was not able to compensate for the deteriorating light conditions. Since z_e was not related to DOC in our study lakes, light intensities ($\bar{E}\,\%$) were low in some lakes compared with the values presented by Houser (2006). In an experimental study by Diehl et al. (2002), covering a wide range of $\bar{E}\,\%$, phytoplankton community production decreased strongly with decreasing $\bar{E}\,\%$. The authors argue that production was not light saturated in any of their treatments and conclude that mixing depth may have profound effects on production and biomass of phytoplankton, as shown in classical marine studies (Sverdrup 1953; Riley 1957). The importance of the mixing depth is also apparent from the comparison of our results to the study by Houser (2006).

In summary, both $\bar{E}\,\%$ and $z_e : z_{eu}$ ratios imply that light may be an important factor limiting phytoplankton biomass production per area in our study lakes. However, phytoplankton growth is considered to be nutrient limited in lakes with high amounts of allochthonous DOC, since bacteria become partially independent of phytoplankton exudates as a growth substrate, and can, because of their favorable surface : volume ratio, monopolize limiting nutrients, usually P (Blomqvist et al. 2001; Bernhardt et al. 2008). This implies that the relative importance of light limitation should increase as nutrient concentrations increase. Yet, it has been shown that high concentrations of DOC can lead to reduced primary production by phytoplankton because of shading (Jones 1992; Carpenter et al. 1998), and there is evidence that light limitation can influence the productivity of the complete lake ecosystem in oligotrophic high-latitude lakes (Karlsson et al. 2009). This latter conclusion was mainly based on a decrease in benthic primary production, whereas phytoplankton would be less affected than benthic producers by PAR-absorbing DOC through active or passive movement in the mixed layer. Nevertheless an unfavorable $z_e : z_{eu}$ ratio would further reduce the food base in lakes. It is unlikely that terrestrial subsidies (DOC entering the bacterial loop) could compensate for the loss of pelagic and benthic primary production if a lake gets browner (Ask et al. 2009; Cole et al. 2006).

Therefore, we suggest that light limitation may be an important factor inhibiting phytoplankton production in small, strongly humic forest lakes, especially considering the fact that our study was conducted during summer, when light conditions are optimal because of high insolation and stable stratification. In spring and autumn, when lakes are unstratified, conditions for phytoplankton should be very unfavorable in brown-colored lakes, at least if the mean depth is larger than the euphotic depth.

Implications for the future—The results from this study imply that light limitation may be an important factor regulating phytoplankton production in small, oligotrophic high-DOC lakes in southern Sweden. In the future, light intensities may decrease further in lakes in this area, because of climate change causing an increase in epilimnion depth, in combination with elevated water color. Concentrations of DOC are currently increasing in lakes in southern Sweden and other parts of the northern hemisphere (Forsberg and Peterson 1990; Findlay 2005; Vuorenmaa et al. 2006), which may be related to climate change (Hongve et al. 2004; Evans et al. 2006) or decreasing sulfur deposition (Monteith et al. 2007; Erlandsson et al. 2008). At the same time, climate change may lead to an increasing number of storm events in southern Sweden (Blennow and Olofsson 2008). Since we found that z_e in lakes in this area is strongly influenced by wind mixing, this may lead to a deeper epilimnion, which will lead to lower light intensities. Modeling indicates that climate change will lead to increased precipitation in parts of Sweden (Rummukainen et al. 2004), which may, as was the case in 2007, lead to increased runoff and DOC leaching from soils, shorter hydraulic residence times in lakes, lower photo-oxidation of chromophoric DOC, and thus lower light intensities in the epilimnion. An increase in DOC and deepening of z_e will thus both contribute to a darkening of the epilimnion in small lakes. This may cause more severe light limitation of phytoplankton, resulting in low biomass, growth, and production, and ultimately lower overall ecosystem production and relatively higher ecosystem respiration, making these lakes more net heterotrophic and thus increasing their contribution of CO_2 to the atmosphere.

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