



Wind drives fast changes of light climate in a large, shallow re-established lake



Kenneth Thorø Martinsen^{a,*}, Theis Kragh^b, Kaj Sand-Jensen^a, Mikkel Madsen-Østerbye^a, Emil Kristensen^a, Jonas Stage Søb^b

^a Freshwater Biological Laboratory, Department of Biology, University of Copenhagen, Universitetsparken 4, 3rd floor, 2100 Copenhagen, Denmark

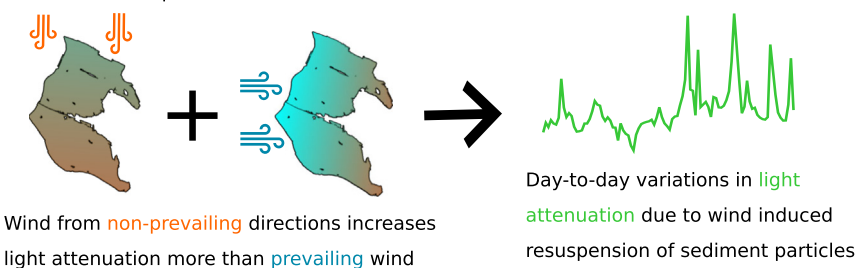
^b Biological Institute, University of Southern Denmark, Campusvej 55, 5230 Odense, Denmark

HIGHLIGHTS

- Pronounced short-term variation in light attenuation (K_d) in a re-established lake
- Variation in K_d is driven by the interaction between wind speed and direction.
- Winds from non-prevailing directions enhanced day-to-day variation in K_d .
- Increasing colonization depth of submerged macrophytes following re-establishment

GRAPHICAL ABSTRACT

The interaction between wind speed and direction influences resuspension in shallow lakes



ARTICLE INFO

Article history:

Received 10 July 2021

Received in revised form 13 October 2021

Accepted 27 October 2021

Available online 30 October 2021

Editor: José Virgílio Cruz

Keywords:

Light attenuation

Ecosystem restoration

Resuspension

High-frequency monitoring

Sediment particles

ABSTRACT

With ever greater frequency, wetlands and shallow lakes that had been diverted for agriculture are being re-established to reduce nutrient loss and greenhouse gas emission, as well as to increase biodiversity. Here, we investigate drivers of water column light attenuation (K_d) at multiple time scales and locations in Lake Fil, Denmark, during the first five years after its re-establishment in 2012. We found that K_d was generally high (overall mean: 3.4 m^{-1}), with resuspended sediment particles and colored dissolved organic matter being the main contributors. Using daily time series of light attenuation recorded at four stations, we used a generalized additive model to analyze the influence of wind speed and direction on K_d . This model explained a high proportion of the variation ($R^2 = 0.62$, RMSE = 0.74 m^{-1} , and MAE = 0.55 m^{-1}) and showed that higher wind speed increased K_d on the same day and, with smaller influence, on the next day. Furthermore, we found a significant influence of wind direction and an interaction between wind speed and wind direction, a combination that suggests that short-term variations in light climate depends on the interplay between wind direction and sources of particles. Wind from non-prevailing directions thus influence K_d more, as it can activate previously deposited particles. The maximum colonization depths of submerged vegetation occurred at ~2–6% of sub-surface light from 2014 to 2016 and peaked at 1.2 m in 2016. The fast, day-to-day variation of K_d in Lake Fil reveals the importance of wind on light climate and in turn biological elements such as phytoplankton and submerged macrophyte development in shallow lakes. The implications are essential for the prior planning and management of future lake re-establishment.

© 2021 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

* Corresponding author.

E-mail address: kenneth.martinsen@bio.ku.dk (K.T. Martinsen).

1. Introduction

During the past 200 years, more than half of Europe's wetlands have been drained and claimed for agriculture (Moreno-Mateos et al., 2012; Zedler and Kercher, 2005). Intensified drainage and stream channelization have resulted in the loss of wetlands in the intensively cultivated European lowland regions (Biggs et al., 2017; Wine and Laronne, 2020). Large shallow lakes have also been drained; in Denmark alone, more than 200 large lakes (~5 lakes per 1000 km² land area), including the country's second and third largest lakes, disappeared between 1780 and 1980 (Hansen, 2014). This trend has changed during recent decades with large investments in both the re-establishment of lakes lost due to anthropological activities and the creation of entirely new lakes.

The long-term loss of wetlands, cultural eutrophication of lakes, and decline of biodiversity have stimulated interest in re-establishing wetlands and lakes and improving their ecological quality. More precise motivations include reducing nutrient export to coastal waters (Audet et al., 2020), improving carbon sequestration (Badiou et al., 2011), enhancing aquatic biodiversity (Mitsch et al., 1998), and creating recreational areas for the public (Hoffmann and Baattrup-Pedersen, 2007). For these reasons, more than 50 larger lakes (>10 ha) have been re-established in Denmark during the past two decades.

Unfortunately, the early development in many re-established lakes is not monitored systematically. Lakes that are re-established on the large phosphorus pools of formerly cultivated soils may face high internal nutrient loading initially accompanied by the release of colored dissolved organic matter (CDOM) that absorbs light in the water column (Kinsman-Costello et al., 2014; Pant and Reddy, 2003; Steinman and Ogdahl, 2011). Often, this results in turbid water columns dominated by phytoplankton that absorbs most of the incoming photosynthetically active radiation (PAR) before it reaches the sediment surface, thus preventing the development of benthic microalgae and submerged macrophytes. In addition to light absorption by photosynthetic pigments and CDOM, scattering of light by suspended organic and inorganic particles are the main determinants of the water column light climate and, summed, yield the diffuse vertical light attenuation coefficient for PAR (K_d , m⁻¹; Kirk (1994)).

K_d is regulated through a complex interplay among biological, physical, and chemical processes occurring both beyond and within the lake. In re-established lakes, much initial CDOM derives from the leaching of flooded terrestrial soils (Kragh et al., 2017). Later, CDOM is mostly derived from terrestrial production in the catchment, which is generally a major cause of high K_d in north-temperate lakes (Karlsson et al., 2009). CDOM is slowly degraded in lakes as a result of photochemical degradation and bacterial mineralization (Madsen-Østerbye et al., 2018). Phytoplankton development is dependent on a range of interacting variables that influence the biomass at a given point in time. The access to major nutrients such as nitrogen and phosphorus, light availability, and water temperature are of particular importance (Wetzel, 2001). Phytoplankton plays two roles with regards to K_d , as the development directly influences the light climate and is itself regulated by the presence of other light attenuating components (Hellström, 1991). Scattering and absorption of light by both phytoplankton and sediment particles suspended in the water column may constitute a large proportion of K_d (Balogh et al., 2009). Resuspension of particles may result from the activities of bottom-feeding fish (Breukelaar et al., 1994) and from near-bottom shear stress that results from wind shear (Reardon et al., 2014). We are especially interested in the latter impact.

In shallow lakes, the contribution of suspended particles in the water column to K_d may be particularly high (Kristensen et al., 1992; Luettich et al., 1990). This is promoted by high wind speeds, which increase near-bottom shear stress and thus resuspension of sediment particles (Reardon et al., 2014); higher speeds can mobilize heavier particles and deeper sediment layers (Bailey and Hamilton, 1997). The efficiency with which surface wind shear is transformed to near-bottom shear

stress depends on wind speed, water depth, and wind direction (Evans, 1994) and the efficiency with which near-bottom shear stress resuspends particles depends on the sheltering of the lakebed. Islands, embayments, or terrestrial vegetation may create sheltered areas that promote particle deposition and hinder resuspension. In short, wind influences horizontal sediment redistribution, and suspension and settling dynamics are modulated by lake bathymetry and morphometry (Håkanson, 1977; Whitmore et al., 1996).

Models based on high temporal resolution data may provide insights not only into the regulation of light climate at different time-scales, but also into the distribution and species richness of submerged macrophytes in turbid lakes. Areas with high macrophyte cover may play a key role in ecosystem functioning by serving as refuges for zooplankton, reducing sediment nutrient release, enhancing particle sedimentation, and competing with phytoplankton for nutrients and, thereby, increasing water transparency (Hilt et al., 2017; Sand-Jensen and Borum, 1991; Scheffer et al., 1993). Moreover, the colonization and development of submerged macrophytes are strongly dependent on K_d , thus creating a positive feedback loop (Hamilton and Mitchell, 1996; Pérez et al., 2013). Improving our understanding of the temporal development and drivers of K_d is especially important in re-established lakes where early management actions could improve future ecological quality.

In the five years following the re-establishment of Lake Fil, high-frequency measurements of K_d collected at four stations enabled us to investigate the spatio-temporal variability of K_d . Due to this lake's shallowness and wind-exposed location, we expected wind to be an important driver of K_d . Specifically, our goals were to: 1) determine the inter- and intra-annual variation in K_d , 2) quantify the influence of wind on K_d , and 3) evaluate the influence of K_d on the development of submerged macrophytes.

2. Methods

2.1. Study site

The study was conducted in Lake Fil, Western Jutland, Denmark (55.70°N, 8.235°E), three km from the North Sea. Lake Fil had been the third-largest lake in Denmark (2185 ha), but it was drained on several occasions starting in 1852. By 1952 it had been totally claimed for agriculture and was intensively cultivated until 2012. Large amounts of inorganic fertilizers and manure were applied, resulting in phosphorus-rich soils.

In 2012, Lake Fil was re-established at approximately one-third of its original size (889 ha) divided into southern and northern basins of equal size. The catchment area is 104 km² with the inlet and outlet located in the southern and northern basins, respectively (Fig. 1). The two basins are separated by a narrow dam and interconnected by a canal through the dam. The lake is shallow, with 1 m in mean depth and 3.5 m in maximum depth. Water retention time averages 70 days (range: 20–180 days). Prior to flooding in autumn 2012, the lakebed was prepared by leaving grain stubble on the fields. These root structures were intended to stabilize the sediment and reduce particle resuspension in and phosphorus release into the water immediately after flooding.

2.2. Data collection

Field measurements were initiated during summer 2013 (seven months after re-establishment). At four open water sites (Fig. 1, St. 1–St. 4), measurements of incoming illuminance (lux) were collected throughout the year, except in cold winter months when the lake surface was frozen. Each station was equipped with two to five sensors (HOBO UA-002-64, Onset Computers) displaced vertically 50–100 cm apart through the water column. Daily water level (2 mm precision) was determined by analyzing differences in pressure recorded by two data loggers, one submerged and the other in the air (HOBO U 20-

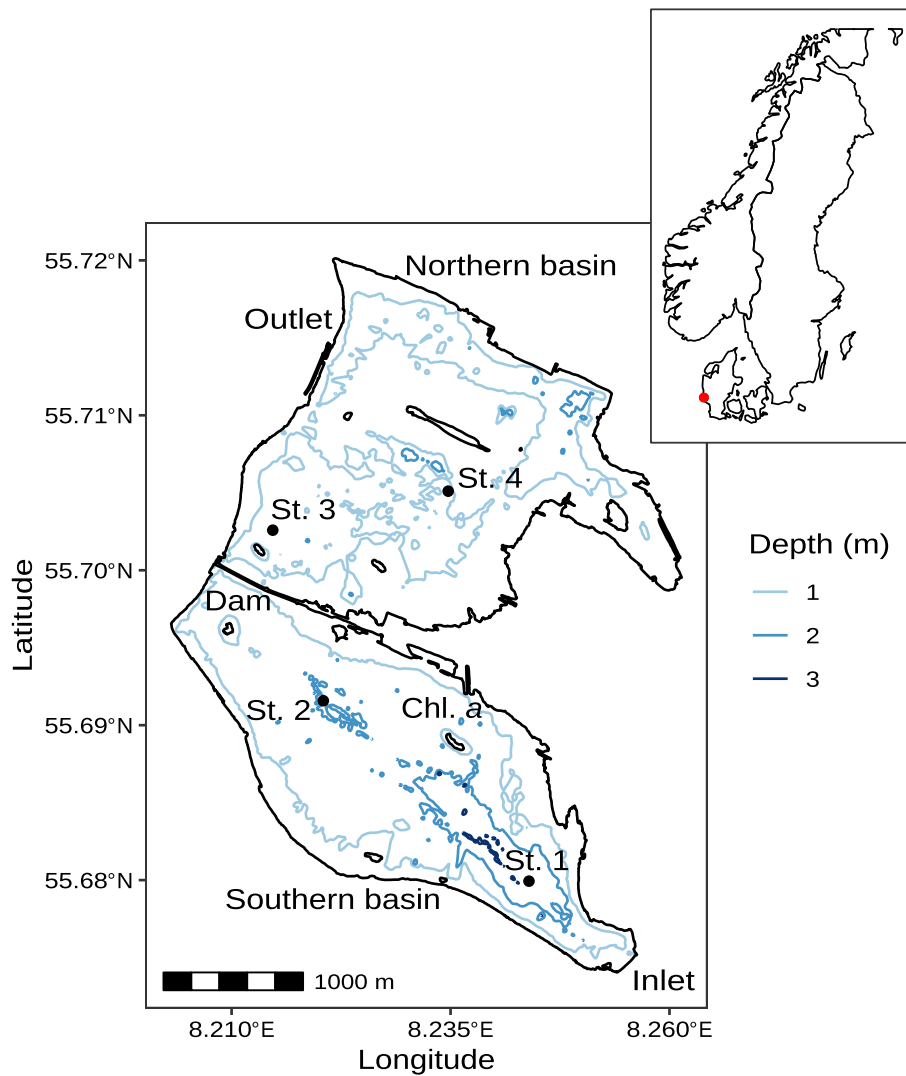


Fig. 1. Map of Lake Fil and its southern and northern basin with position of light measurement stations (St. 1–St. 4), dam, chlorophyll *a* station (Chl. *a*), inlet, and outlet. Contour lines are shown for 1.0 m intervals. Water level was measured at the dam and water samples were collected regularly at the inlet, dam and outlet.

001–04, Onset Computers). High-frequency (10 min) light measurements were used to determine daily values of K_d . For each day and station, incoming illuminance was summed and converted from lux to incoming irradiance (I , PAR 400–700 nm) using a linear model without an intercept ($I = \text{lux} \cdot 0.00975$, $n = 699$, $p < 0.001$, $R^2 = 0.996$, Fig. S1) fitted from concurrent lux and I measurements on land (HOBO S-LIA-M003, Onset Computers). When daily incoming irradiance (I_2) was available at three or more depths (z), K_d was calculated as the slope of linear model fits (Eq. (1)) and from Eq. (2) when available at only two depths (I_1 at z_1 and I_2 at z_2 ; Kirk (1994)).

$$\log(I_z) = K_d \cdot z + \log(I_0) \quad (1)$$

$$K_d = \frac{\log(I_2) - \log(I_1)}{z_2 - z_1} \quad (2)$$

Some low-quality readings were observed, mainly due to excessive fouling of some sensors during certain periods. We used four criteria to identify and then remove low-quality observations: total daily illuminance < 500 lx, $< 10\%$ difference in incoming illuminance between top and bottom sensors (when applying Eq. (2)), observations with R^2 values < 0.5 (when applying Eq. (1)), and K_d values $< 0 \text{ m}^{-1}$. In all, 10% of days with measurements were discarded based on the four criteria or only having readings from one sensor.

High-frequency (10 min) meteorological data measured at 2 m above the ground were obtained from a nearby (18 km) meteorological station operated by the Danish Meteorological Institute (DMI, 2021) to calculate daily wind speed and direction averages.

Phytoplankton chlorophyll *a* fluorescence was measured continuously in the southern basin (“Chl. *a*” site in Fig. 1) using a CYCLOPS-7 fluorescence probe (Turner Design, CA, USA) placed 30 cm below the water surface. The fluorescence signal was calibrated against water samples analyzed for chlorophyll *a* by extraction in ethanol and measurement on a Shimadzu UV-1800 spectrophotometer (Jespersen and Christoffersen, 1987).

The maximum colonization depths of submerged macrophytes were determined from visual inspection of side-scan imagery collected during July and August in all years. We collected side-scan imagery by traversing the lake in parallel paths with up to 50 m distance intervals with a boat using a Lowrance HDS-12 Gen3 sonar (Navico, Egersund, Norway) equipped with a Lowrance Hybrid Dual Imaging Skimmer Transducer operating at 200 KHz and a StructureScan HD transducer. The collected side-scan imagery was assembled in Reefmaster 2.0 (ReefMaster Software Ltd., United Kingdom). Using coordinates of the observed submerged macrophyte patches, the maximum colonization depths were calculated from the average water level from April till August every year.

Water samples were collected every other week from the canal connecting the two basins (Fig. 1). Nutrient concentrations were

measured using standard methods (American Public Health Association, 1971). For light absorbance measurements, water was filtered through pre-combusted GF/F filters (0.7 μm), and absorbance at 440 nm (A_{440}) was measured in 1 cm cuvettes ($L = 0.01$ m) on a spectrophotometer (UV-1800 Shimadzu) as a proxy of CDOM. The light attenuation coefficient (a_{440} , m^{-1}) at 440 nm was determined (Eq. 3) after subtracting the absorbance at 750 nm (A_{750}).

$$a_{440} = \frac{2.303 \cdot (A_{440} - A_{750})}{L} \quad (3)$$

In examining the relative contribution of the optical components to K_d , we used empirical estimates of specific light absorption for CDOM, chlorophyll a , and water itself. For CDOM, we used the value from Balogh et al. (2009), which is based on measurements in shallow lakes; for chlorophyll a , we used the mean value of a literature survey (Krause-Jensen and Sand-Jensen, 1998), and for water, we used the value reported by Smith and Baker (1978). After subtraction of the attenuation due to CDOM (K_{CDOM}), chlorophyll a ($K_{Chl. a}$), and water (K_{water}) components from K_d , the remainder is the estimated

attenuation due to organic and inorganic particles ($K_{particles}$) in the water column (Eq. (4)). We determined the contribution of each component to K_d only for the southern basin, where chlorophyll a was measured.

$$K_d = K_{CDOM} + K_{Chl. a} + K_{water} + K_{particles} \quad (4)$$

2.3. Statistical analysis

We used generalized additive models (GAM) to quantify the influence of wind speed and direction on K_d . GAM enable different types of smoothing functions to be fitted to predictor variables and include correlation structures accounting for the residuals' temporal dependence, often prominent in time series data (Pedersen et al., 2019). Results from initial experiments using linear mixed models violated statistical assumptions and were deemed unsatisfactory. Therefore, we used a GAM approach that has proven suitable for modeling time series data by means of different residual error structures and the inclusion of non-linear relationships (Simpson, 2018; Yang and Moyer, 2020). The use of

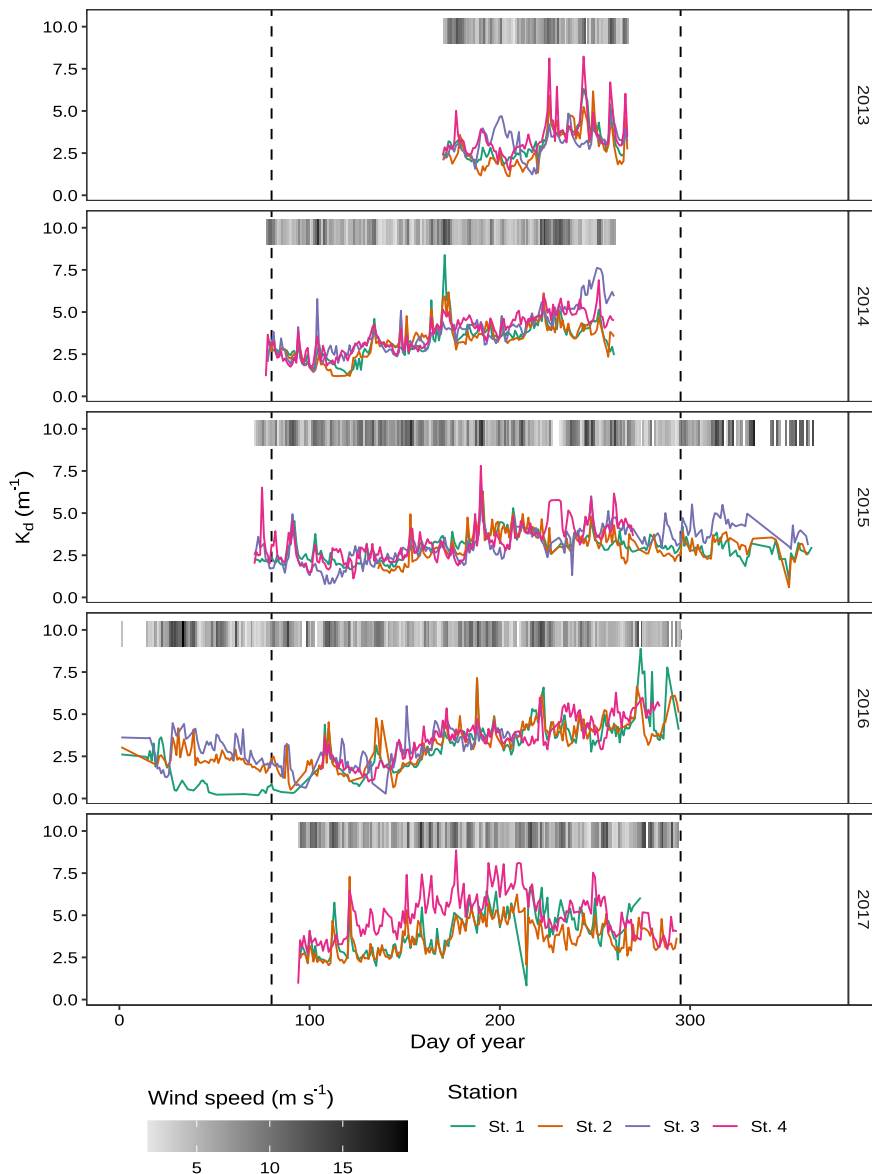


Fig. 2. Daily light attenuation coefficient (K_d) at each site (solid lines) and daily mean wind speed (horizontal bar) during five years. The vertical stippled lines enclose the period used for modeling.

GAM and smoothing functions can also be justified from the expected relationship between K_d and wind speed, i.e., variation in K_d is expected to follow, but not instantaneously, sustained changes in wind speed.

We used data collected from calendar-days 80–295, the main growing season (late March–late October; Middelboe and Markager, 1997; van Dijk et al., 1992), where the overlap of data across years was largest, resulting in 3037 observations over the five years. The initial model fits included: station, wind speed on the same day (t_0) and 1–3 days before (t_{-1} , t_{-2} and t_{-3}), wind direction, the interaction between wind speed at t_0 and wind direction, and inter- and intra-annual time trends. From initial GAM fits, we assessed the significance of smoothing and included non-significant smooth terms as linear predictors. ‘Station’ was included as a random effect, wind speed at t_0 was used as thin plate regression splines, wind direction as cyclic cubic regression splines, and their interaction as a tensor interaction smooth. Seasonal and inter-annual effects were included using a day of the year and year smooth terms, respectively, and the inclusion of a tensor interaction smooth between the two was also tested. Initial GAM fits revealed high residual autocorrelation. Therefore, we compared the performance

of different correlation structures using the Akaike information criterion (AIC; Burnham and Anderson (2002)). The continuous-time covariate-order-one autocorrelation structure was found to provide the best fit. This was followed by using AIC to compare multiple candidate models containing different combinations of predictors. Model diagnostics were performed using autocorrelation and partial autocorrelation functions, along with residual plots. GAM were fitted using the mgcv R-package (Wood, 2017). All statistical analyses were performed using the R programming language (R Core Team, 2021), and all scripts for the analysis are available from an online repository (<https://github.com/KennethTM/FilsoLight>).

3. Results

3.1. Spatio-temporal variability of light attenuation

Water column K_d exhibited a large variation (range: 0.2–8.9 m^{-1}) and averaged 3.4 m^{-1} over the five years (Fig. 2). The mean water depth where only 10% of incoming irradiance remained ($z_{10\%}$) was 0.8 m. Sudden increases in K_d generally occurred simultaneously at all

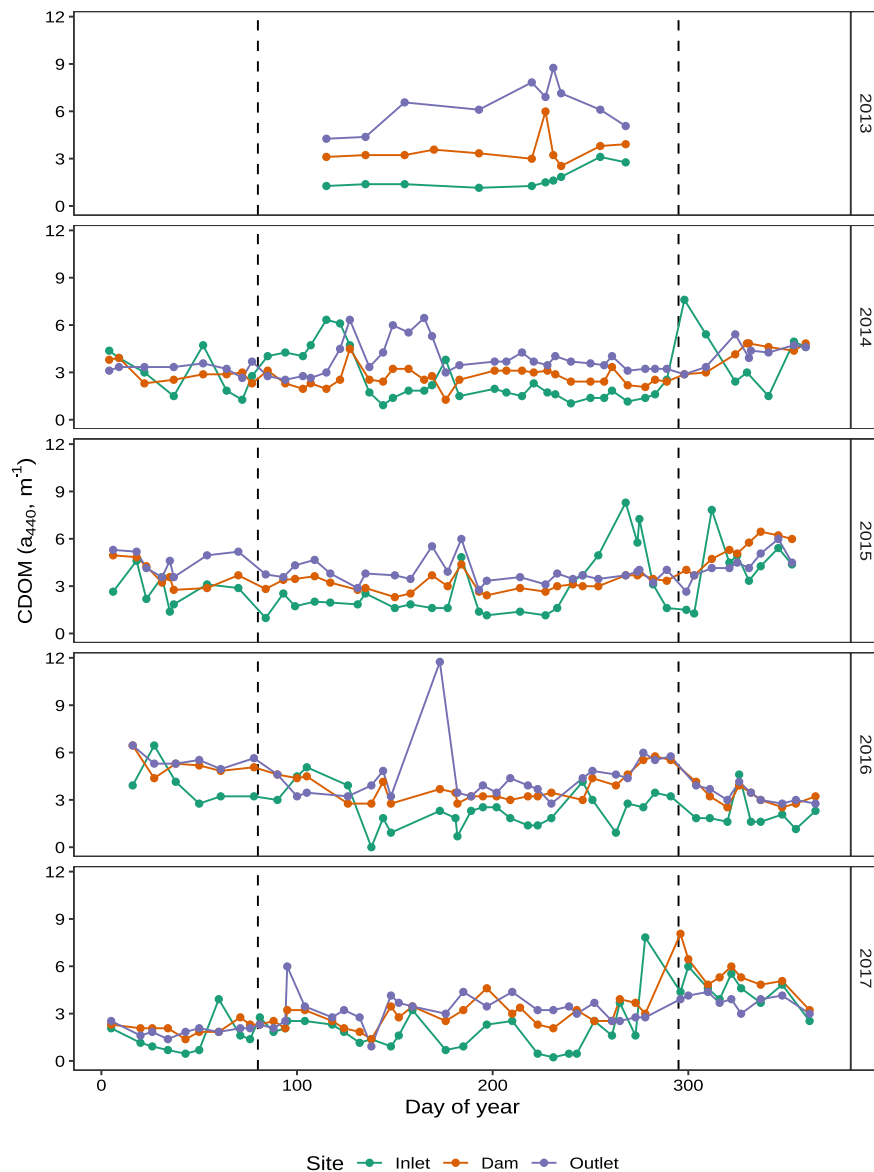


Fig. 3. CDOM expressed as the light absorption coefficient at 440 nm (a_{440}) sampled at the inlet, outlet and the canal through the dam, connecting the two lake basins, through the five years.

stations, suggesting a common external driver. Variations on both short (days) and long (weeks) time scales are prominent in the time series. Mean K_d was similar at St. 1 (3.2 m^{-1}), St. 2 (3.3 m^{-1}), and St. 3 (3.2 m^{-1}), but was consistently higher at St. 4 (3.9 m^{-1}), thus increasing with distance from the inlet.

3.2. Variables influencing light attenuation

During the first summer in Lake Fil, the water was much clearer at the inlet than at the outlet: mean a_{440} increased rapidly from the inlet (1.7 m^{-1}) to the dam-connection between the two basins (3.5 m^{-1}) and on to the outlet (6.3 m^{-1}). This was likely due to the accumulated release of CDOM from the soil and crop stubble that comprised the newly flooded lakebed (Fig. 3). The difference between inlet and outlet a_{440} decreased over the following years. Seasonal variations in a_{440} were not pronounced, though slightly lower values were observed during summer (mean: 3.1 m^{-1}) compared to autumn, winter, and spring (mean: 3.5 m^{-1}). Pronounced increases in CDOM at the inlet could occur in late summer and autumn following precipitation events from the catchment.

Chlorophyll *a* levels were generally low (overall mean $9.6 \mu\text{g L}^{-1}$; range $0.02\text{--}77 \mu\text{g L}^{-1}$) when considering the high lake nutrient levels (Fig. 4A–B). Mean (\pm SD, N) lake nutrient concentrations, measured bi-weekly from 2013 through 2017, were $12 (\pm 26, 370) \mu\text{g P L}^{-1}$ as PO_4^{3-} , $86 (\pm 146, 359) \mu\text{g P L}^{-1}$ as total phosphorus, $724 (\pm 707, 370) \mu\text{g N L}^{-1}$ as NO_3^- , and $2135 (\pm 1285, 359) \mu\text{g N L}^{-1}$ as total nitrogen. Chlorophyll *a* rapidly developed during phytoplankton blooms of limited duration ($\sim 2\text{--}3$ weeks) throughout the growing season. High values

of chlorophyll *a* could occur between app. $5\text{--}20^\circ\text{C}$ with no apparent effect of water temperature (Fig. S2).

Winds measured at a nearby meteorological station were relatively strong, with mean daily wind speeds of 7.2 m s^{-1} (range: $1.3\text{--}20.7 \text{ m s}^{-1}$). Wind speeds were highest during winter and lowest during summer. Westerly winds were prevailing, and the wind was rarely from the north (Fig. 4C–D). The morphometry of Lake Fil makes it very exposed to wind from the most prevailing wind directions.

3.3. Modeling light attenuation

To select a generalized additive model for further analysis, we evaluated a range of candidate models with different combinations of predictor variables. The top three models performed very similarly (within 2.60 AIC units), and they differed only in the number of lagged wind speed terms (Table 1). We selected the rank one model for further analysis. This model contained the fewest terms of the three best ranking models, namely two wind speed terms (at the day t_0 and the day t_{-1} before light measurement), wind direction and, a wind direction-wind speed interaction term, and inter- and intra-annual temporal terms. This GAM accounted for variations in K_d with an R^2 of 0.62, root-mean-squared-error (RMSE) of 0.74 m^{-1} , mean-absolute-error (MAE) of 0.55 m^{-1} . The predicted vs. the observed values were spread evenly around the 1:1 line (Fig. 5).

Based on this GAM, it was possible to quantify the influence of wind speed and direction on K_d . Wind speed at t_0 had the strongest influence on K_d , which increased rapidly as wind speeds exceeded $\sim 5 \text{ m s}^{-1}$ (Fig. 6A). K_d also depended on wind speed on the previous day, t_{-1} (Fig. 6B). However, the effect of wind speed was

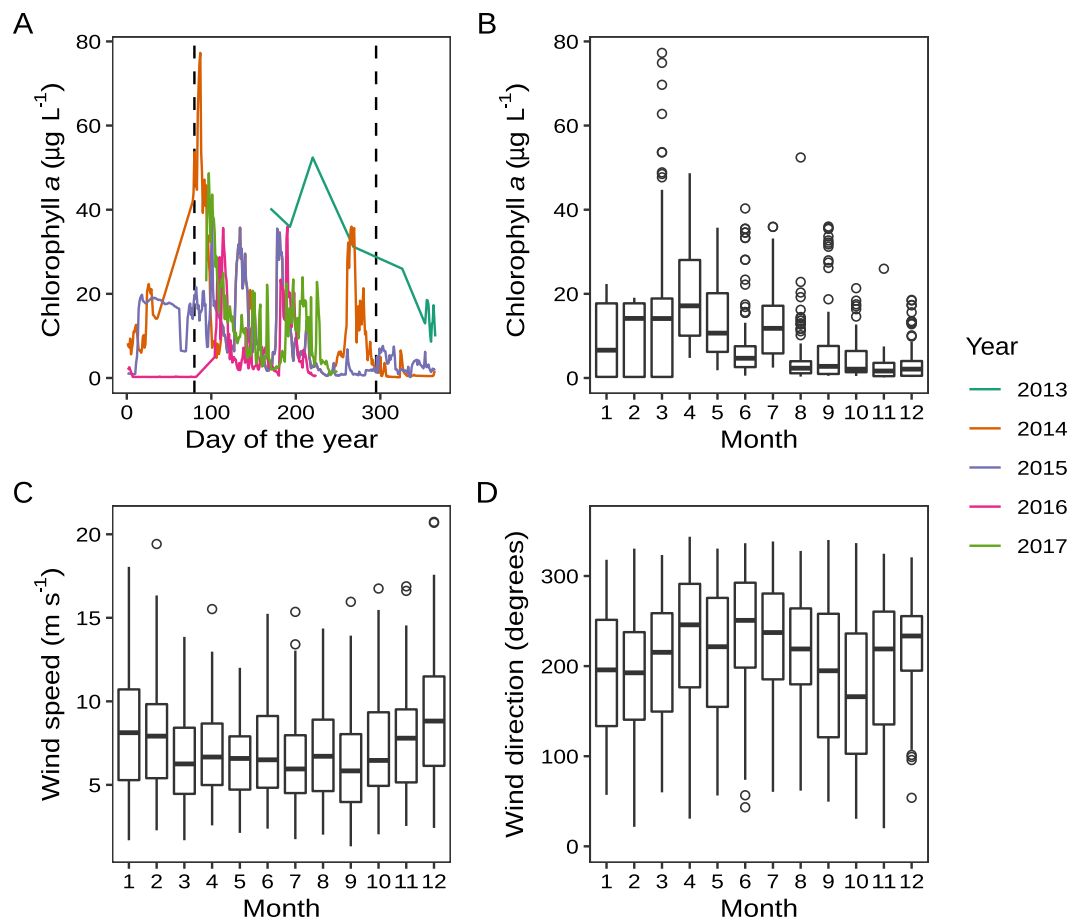


Fig. 4. Variables influencing light attenuation across the year: A) Daily mean chlorophyll *a* colored by year, and B–D) Daily mean chlorophyll *a*, wind speed, and direction summarised as box-plots for each month across the five years. Box-plots show median (solid horizontal line), 25% and 75% quartiles (upper and lower hinge), lines extending to one and a half times the inter-quartile range (upper and lower whisker) and observations outside this range (points).

Table 1

Model selection table for the top-four candidate GAM models. Only some terms are included in the table as the smoothed terms, time (inter- and intra-annual variation), wind speed and wind direction are included in all the best candidate models. For each model df (number of parameters), AIC, Δ AIC, and AIC weights are reported. For parametric terms (wind speed lag t_{-1} to t_{-3}), the effect size is also included.

Model rank	Intercept	Wind speed & wind direction interaction	Wind speed (t_{-1})	Wind speed (t_{-2})	Wind speed (t_{-3})	df	AIC	Δ AIC	AIC weight
1	3.34	+	0.056			17	5082.9	0	0.6
2	3.32	+	0.057		0.002	18	5084.8	1.86	0.24
3	3.29	+	0.057	0.005	0.002	19	5085.5	2.6	0.16
4	3.23		0.057			15	5098.1	15.2	0

modulated by wind direction: K_d was larger when winds came from northerly directions, while the prevailing westerly winds were less influential (Fig. 6C–D). This pattern reflects the interplay between source and process limitation, i.e., the availability of sediment particles that are susceptible to resuspension at a given wind speed. For example, the difference in predicted K_d at a wind speed of 5 m s^{-1} from the prevailing (median wind direction of 227 degrees) and north (0 degrees) is only 0.04 m^{-1} but this difference increases drastically to 0.5 and 1.3 m^{-1} at wind speeds of 10 and 15 m s^{-1} . The influence of intra-annual variation (Fig. 6E) is strongest during summer and is likely due to the combined influences of phytoplankton and reduced lake water volume. The inter-annual trend (Fig. 6F) shows a decrease in K_d during the first three years, followed by increases in 2016 and 2017.

3.4. Partitioning of light attenuation components

Using the measured a_{440} and chlorophyll a concentration in the southern basin, we determined the relative contribution of each component to K_d . K_d was generally dominated by the contribution to light attenuation from particles (mean: 52.2%) and CDOM (mean: 39.8%) with a minor periodic contribution from chlorophyll a (mean: 6.8%) and water (mean: 1%; Fig. S3). Most of the time, phytoplankton chlorophyll a was not a major contributor to K_d , but during short-lived blooms generally lasting a few weeks, chlorophyll a reached about $35 \mu\text{g L}^{-1}$ corresponding to an attenuation of $\sim 0.52 \text{ m}^{-1}$ and increased the contribution accordingly. The particles that dominate K_d are most likely suspended in the water column as a consequence of wind-induced resuspension.

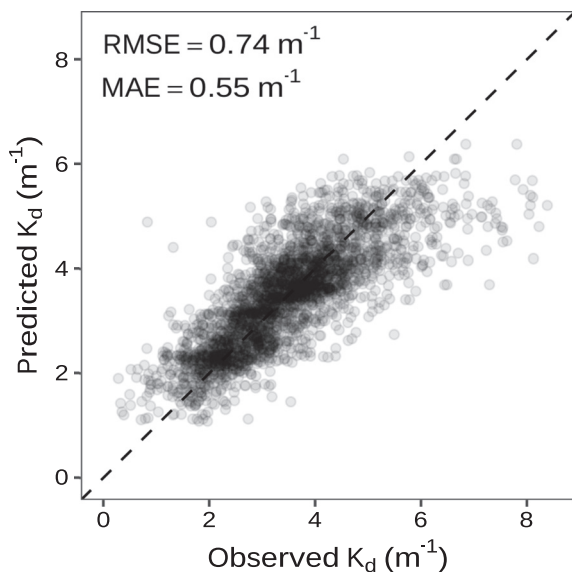


Fig. 5. Observed and predicted K_d by the selected GAM, root-mean-squared-error (RMSE), mean-absolute-error (MAE), and the 1:1 relationship (stippled line).

3.5. Distribution of submerged macrophytes

Submerged macrophytes rapidly colonized Lake Fil, extending to 0.5 m the first summer and steadily increasing during the following three years, reaching 1.2 m in 2016. Their maximum colonization depth generally followed that of light availability (Fig. 7). The water depth with 10% of incoming irradiance ($z_{10\%} = 2.3 \cdot K_d^{-1}$) increased during the lake's first four years and dropped in 2017, reducing the depth distribution of submerged macrophytes. During 2015–2016, the submerged macrophytes reached a depth where approximately 2–6% of incoming radiation was present. The observed maximum colonization depth and $z_{10\%}$ trends were consistent with the inter-annual trend term estimated with the GAM (Fig. 6 F), with increasing K_d from 2016 to 2017.

4. Discussion

4.1. The light climate in re-established lakes

Re-established lake ecosystems are often highly dynamic, and their development is difficult to predict. Just three years after re-establishment, Lake Fil supported a very high species richness, including 40 different species of aquatic macrophytes (Baastrup-Spohr et al., 2016). This high richness was maintained seven years after re-establishment. As re-established lakes age beyond 20 years, more scattered observations suggest that macrophyte richness may decrease (Sø et al., 2020). This apparent trend underscores that monitoring the early development of new lakes is essential in order to understand the ecology and biodiversity and improve the design and early management depending on the aims of the lake restoration (Audet et al., 2020).

Prior to the re-establishment of Lake Fil, we expected that high nutrient levels would enable phytoplankton to dominate in the new lake. We were mistaken. As a consequence of the lake's wind exposure, low water depths, and short water retention times, large quantities of nutrients and organic matter were rapidly flushed out of the system (Kragh et al., 2017). Rapid nutrient loss has also been observed in other restored wetlands (Kinsman-Costello et al., 2014; Steinman and Ogdahl, 2011). In the case of Lake Fil, nutrient loss was further promoted by wind-induced wave action and physical disturbance of surface sediment, resulting in resuspension of sediment particles and, thereby, further nutrient release (Hamilton and Mitchell, 1996; Søndergaard et al., 2003). In combination with CDOM, these resuspended particles are the main contributors to K_d in Lake Fil.

4.2. Contributions of CDOM and chlorophyll a to K_d

The highest CDOM absorption coefficients in both basins were observed in Lake Fil's first summer (2013) with decreasing values in 2014–2017. The higher a_{440} values were likely a result of lakebed organic carbon and grain-stubble leaching humic compounds to the water after flooding (Zak et al., 2018). This dynamic countered the effects of grain stubble root structures that, as intended, stabilized lakebed sediment and initially resulted in lower wind-induced sediment

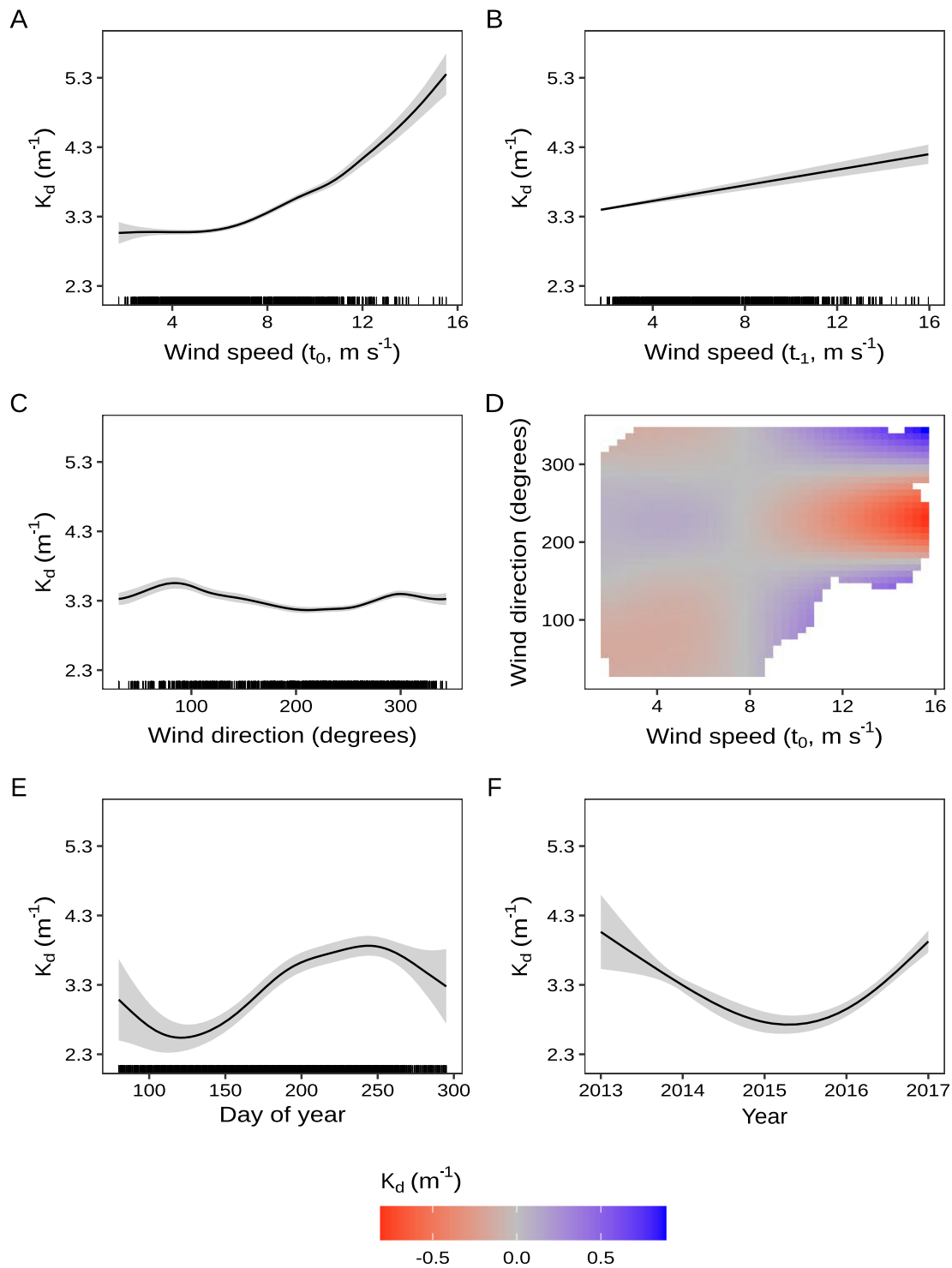


Fig. 6. The relative influence of the predictor terms included in the selected GAM on K_d : A) wind speed at t_0 , B) wind speed at t_{-1} , C) wind direction, D) interaction of wind speed and wind direction, and E) contribution of intra-year variation and F) long-term trend. The "rug" along the x-axis in figures A, B, C, and E show individual observations.

resuspension (Kragh et al., 2017). The gradual release of sediment CDOM continued throughout the first five years, with CDOM generally increasing from lake inlet to outlet, suggesting that in-lake sources are still contributing to this organic matter pool. However, the largest source of seasonal variation in CDOM appears to be pulse events at the inlet determined by precipitation patterns and catchment processes (Kragh et al., 2020). The CDOM contribution to K_d is variable, but generally changes on longer time-scales (seasons) than that of chlorophyll *a* or suspended particles.

Although chlorophyll *a* is expected to be high when phosphate and nitrogen are as concentrated as they are at Lake Fil (Schallenberg and Burns, 2004), the low observed chlorophyll *a* levels are likely due to light limitation caused by high CDOM and particle concentrations in the water column (Jones et al., 1996; Karlsson et al., 2009). Time periods (at the scale of weeks) with low wind speeds and, consequently, lower light attenuation by resuspended particles, are likely required for larger phytoplankton blooms to develop.

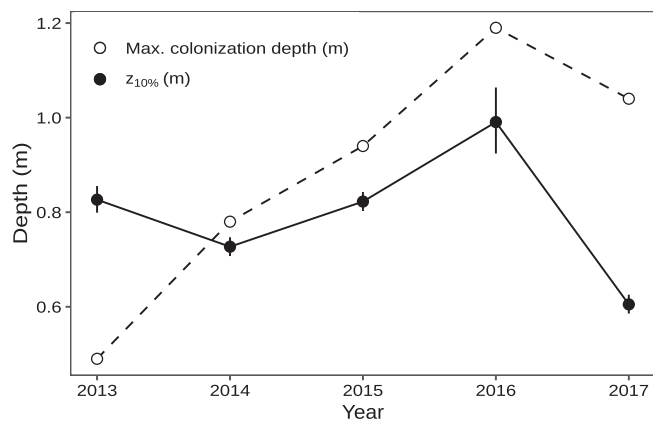


Fig. 7. Observed maximum colonization depth of submerged macrophytes (open circle) and annual mean depth where 10% of incoming irradiance is left ($z_{10\%}$, closed circle) with bootstrapped (1000 repetitions) 95% confidence intervals for each year.

4.3. The influence of wind induced resuspension

The selected GAM shows that wind speed was an important driver of short-term (day-to-day) variation in K_d and is likely an important process in other wind-exposed shallow lakes. The model showed that higher wind speed resulted in higher K_d on both that day and, to a lesser degree, the following day. This is expected, as increasing wind speeds result in higher near-bottom shear stress, which enables particles of increased size and deeper position in sediments to be suspended in the water column (Valipour et al., 2017). Observations in other systems confirm that wind is the major contributor to near-bottom shear stress during resuspension events (Reardon et al., 2014). Also, high wind events have carry-over effects that continue to influence K_d for hours or even days after the event. The abrupt increase in K_d during windy periods was evident at all stations and, because meteorological data can be used to forecast wind speed, it is also possible to predict K_d (Hamilton and Mitchell, 1996).

Importantly, the model also shows that wind direction modulates the influence of wind speed on K_d . This phenomenon has also been observed in other shallow lakes (Bengtsson et al., 1990; Löfstedt and Bengtsson, 2008). It is likely a consequence of differences in sediment distribution and composition, which determine the quantity of resuspendable particles at a given wind speed. Sediment composition is influenced by the prevailing wind directions, lake morphometry, and bathymetry (Whitmore et al., 1996). Wind direction from non-prevailing directions may thus resuspend recently deposited particles or erode the softer sediments more easily. In the case of the shallow Lake Fil, a light fraction of the sediment particles is likely involved, repeatedly, in the majority of resuspension events (Luettich et al., 1990). All of these conditions can be ameliorated during the design of to-be-re-established lakes. By considering historical meteorological data during the planning phase, export or settlement of organic particles can be improved by choices taken regarding lake morphometry and bathymetry. Such actions could also include establishing islands or pits that enable particle settlement and thus facilitate more transparent water (Sø et al., 2021).

4.4. Influence of light climate on submerged macrophyte distribution

Light availability is essential for the colonization and distribution of submerged macrophytes. Furthermore, the development of submerged macrophytes provides important feedback effects on K_d and ecosystem functioning (Jeppesen, 1998; Sand-Jensen and Borum, 1991). This presents an interesting interplay between wind and macrophyte development. When light and nutrient

requirements are met, wind-induced resuspension may promote development by reducing organic matter and improving texture in sediment (Barko and Smart, 1986). Once established, submerged macrophyte stands decrease sediment resuspension by reducing flow velocities and stabilizing sediments (Sand-Jensen, 1998). On the other hand, high mechanical stress in wind-exposed lakes may restrict the development of submerged macrophyte stands. Most important, however, is that temporal changes in light availability enable macrophyte colonization and growth. Rooney and Kalff (2000) show that biomass distribution is affected by inter-annual variations. Good light conditions early in the growing season resulted in increasingly deep macrophyte colonization. While short-term changes in K_d are driven directly by changes in wind speed and direction, high wind speeds during late winter and early spring may also hamper early colonization and development of submerged macrophytes in Lake Fil. This may be reinforced when high CDOM levels appear in spring, as they did in 2017 in Lake Fil. Nonetheless, the re-established Lake Fil supports one of the highest species richness of aquatic plants in Denmark (Baastrup-Spohr et al., 2016). This is likely due to the lake's location in a species-rich region and the existence of a dynamic coastal zone, where submerged macrophytes can colonize in extensive shallow waters that are kept free of tall emergent swamp and reed vegetation by extensive water level fluctuations (50–100 cm annually), wave exposure, and cattle grazing (Baastrup-Spohr et al., 2016).

5. Conclusions

The intense monitoring in the re-established Lake Fil highlights the importance of wind-induced resuspension on day-to-day variations in light climate in shallow lakes. Light attenuation in Lake Fil was sufficient to suppress the development of phytoplankton, despite high nutrient levels, and the main contributors to light attenuation were resuspended particles and CDOM. High wind speeds increased light attenuation, though this effect was modulated by wind direction, as wind shifts and wind from the non-prevailing directions increased light attenuation more than wind from the prevailing directions. This indicates that a small proportion of the lake's particles is regularly redistributed by wind, which can result in fast changes in light climate. During the first five years, K_d decreased and submerged macrophytes grew increasingly deep. Submerged macrophytes did not respond instantaneously to changes in the light climate due to the time delay for growth. This was evident in the first summer following re-establishment (2013) where macrophytes grew shallower than expected from the light climate, and in 2017 where growth was observed deeper than what the prevailing light climate predicted.

CRedit authorship contribution statement

Kenneth Thorø Martinsen: Conceptualization, Data curation, Methodology, Formal analysis, Software, Visualization, Writing – original draft, Writing – review & editing. **Theis Kragh:** Formal analysis, Conceptualization, Investigation, Data curation, Project administration, Funding acquisition, Writing – review & editing. **Kaj Sand-Jensen:** Conceptualization, Methodology, Funding acquisition, Writing – original draft, Writing – review & editing. **Mikkel Madsen-Østerbye:** Investigation, Data curation, Writing – review & editing. **Emil Kristensen:** Investigation, Writing – review & editing. **Jonas Stage Sø:** Formal analysis, Investigation, Data curation, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgement

We thank the Aage V. Jensen Nature Foundation for grants to KSJ and TK. We thank the Villum Foundation via the Center of Excellence for Lake Restoration (CLEAR) and the Independent Research Fund Denmark (0217-00112B) for grants to KSJ. We thank David Stuligross for comments and linguistic corrections.

Appendix A. Supplementary figures

Supplementary figures to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2021.151354>.

References

- American Public Health Association, 1971. *Standard Methods for the Examination of Water and Wastewater*. American Public Health Association, New York.
- Audet, J., Zak, D., Bidstrup, J., Hoffmann, C.C., 2020. Nitrogen and phosphorus retention in Danish restored wetlands. *Ambio* 49, 324–336. <https://doi.org/10.1007/s13280-019-01181-2>.
- Baastrup-Spohr, L., Kragh, T., Petersen, K., Moeslund, B., Schou, J.C., Sand-Jensen, K., 2016. Remarkable richness of aquatic macrophytes in 3-years old re-established Lake Fil, Denmark. *Ecol. Eng.* 95, 375–383. <https://doi.org/10.1016/j.ecoleng.2016.06.081>.
- Badiou, P., McDougal, R., Pennock, D., Clark, B., 2011. Greenhouse gas emissions and carbon sequestration potential in restored wetlands of the Canadian prairie pothole region. *Wetl. Ecol. Manag.* 19, 237–256. <https://doi.org/10.1007/s11273-011-9214-6>.
- Bailey, M.C., Hamilton, D.P., 1997. Wind induced sediment resuspension: a lake-wide model. *Ecol. Model.* 99, 217–228. [https://doi.org/10.1016/S0304-3800\(97\)01955-8](https://doi.org/10.1016/S0304-3800(97)01955-8).
- Balogh, K.V., Németh, B., Vörös, L., 2009. Specific attenuation coefficients of optically active substances and their contribution to the underwater ultraviolet and visible light climate in shallow lakes and ponds. *Hydrobiologia* 632, 91–105. <https://doi.org/10.1007/s10750-009-9830-9>.
- Barko, J.W., Smart, R.M., 1986. Sediment-related mechanisms of growth limitation in submersed macrophytes. *Ecology* 67, 1328–1340. <https://doi.org/10.2307/1938689>.
- Bengtsson, L., Hellström, T., Rakoczi, L., 1990. Redistribution of sediments in three Swedish lakes. *Hydrobiologia* 192, 167–181. <https://doi.org/10.1007/BF00006012>.
- Biggs, J., von Fumetti, S., Kelly-Quinn, M., 2017. The importance of small waterbodies for biodiversity and ecosystem services: implications for policy makers. *Hydrobiologia* 793, 3–39. <https://doi.org/10.1007/s10750-016-3007-0>.
- Breukelaar, A.W., Lammens, E.H.R.R., Breteler, J.G.P.K., Tátrai, I., 1994. Effects of benthivorous bream (*Abramis brama*) and carp (*Cyprinus carpio*) on sediment resuspension and concentrations of nutrients and chlorophyll a. *Freshw. Biol.* 32, 113–121. <https://doi.org/10.1111/j.1365-2427.1994.tb00871.x>.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, New York.
- DMI, 2021. Danish Meteorological Institute. www.DMI.dk/friedata accessed 7. April 2021.
- Evans, R.D., 1994. Empirical evidence of the importance of sediment resuspension in lakes. *Hydrobiologia* 284, 5–12. <https://doi.org/10.1007/BF00005727>.
- Håkanson, L., 1977. The influence of wind, fetch, and water depth on the distribution of sediments in Lake Vänern, Sweden. *Can. J. Earth Sci.* 14, 397–412. <https://doi.org/10.1139/e77-040>.
- Hamilton, D.P., Mitchell, S.F., 1996. An empirical model for sediment resuspension in shallow lakes. *Hydrobiologia* 317, 209–220. <https://doi.org/10.1007/BF00036471>.
- Hansen, K., 2014. *People and Tales of the Lost Land (in Danish)*. Narayana Press, Odder, Denmark.
- Hellström, T., 1991. The effect of resuspension on algal production in a shallow lake. *Hydrobiologia* 213, 183–190. <https://doi.org/10.1007/BF00016421>.
- Hilt, S., Brothers, S., Jeppesen, E., Veraart, A.J., Kosten, S., 2017. Translating regime shifts in shallow lakes into changes in ecosystem functions and services. *Bioscience* <https://doi.org/10.1093/biosci/bix106>.
- Hoffmann, C.C., Baastrup-Pedersen, A., 2007. Re-establishing freshwater wetlands in Denmark. *Ecol. Eng.* <https://doi.org/10.1016/j.ecoleng.2006.09.022>.
- Jeppesen, E., 1998. *The structuring role of submerged macrophytes in lakes*. Ecological Studies. Springer, New York.
- Jespersen, A.-M., Christoffersen, K., 1987. Measurements of chlorophyll—a from phytoplankton using ethanol as extraction solvent. *Arch. Hydrobiol.* 109, 445–454.
- Jones, R., Young, J., Hartley, A., Bailey-Watts, A., 1996. Light limitation of phytoplankton development in an oligotrophic lake—Loch Ness, Scotland. *Freshw. Biol.* <https://doi.org/10.1111/j.1365-2427.1996.tb01767.x>.
- Karlssohn, J., Byström, P., Ask, J., Ask, P., Persson, L., Jansson, M., 2009. Light limitation of nutrient-poor lake ecosystems. *Nature* 460, 506–509. <https://doi.org/10.1038/nature08179>.
- Kinsman-Costello, L.E., O'Brien, J., Hamilton, S.K., 2014. Re-flooding a historically drained wetland leads to rapid sediment phosphorus release. *Ecosystems* 17, 641–656. <https://doi.org/10.1007/s10021-014-9748-6>.
- Kirk, J.T., 1994. *Light and Photosynthesis in Aquatic Ecosystems*. Cambridge University Press, Cambridge.
- Kragh, T., Sand-Jensen, K., Petersen, K., Kristensen, E., 2017. Fast phosphorus loss by sediment resuspension in a re-established shallow lake on former agricultural fields. *Ecol. Eng.* <https://doi.org/10.1016/j.ecoleng.2017.07.026>.
- Kragh, T., Martinsen, K.T., Kristensen, E., Sand-Jensen, K., 2020. From drought to flood: sudden carbon inflow causes whole-lake anoxia and massive fish kill in a large shallow lake. *Sci. Total Environ.* 739, 140072. <https://doi.org/10.1016/j.scitotenv.2020.140072>.
- Krause-Jensen, D., Sand-Jensen, K., 1998. Light attenuation and photosynthesis of aquatic plant communities. *Limnol. Oceanogr.* 43, 396–407. <https://doi.org/10.4319/lo.1998.43.3.0396>.
- Kristensen, P., Søndergaard, M., Jeppesen, E., 1992. Resuspension in a shallow eutrophic lake. *Hydrobiologia* 228, 101–109. <https://doi.org/10.1007/BF00006481>.
- Lövstedt, C.B., Bengtsson, L., 2008. The role of non-prevailing wind direction on resuspension and redistribution of sediments in a shallow lake. *Aquat. Sci.* 70, 304–313. <https://doi.org/10.1007/s00027-008-8047-8>.
- Luetlich, R.A., Harleman, D.R.F., Somlyódy, L.A., 1990. Dynamic behavior of suspended sediment concentrations in a shallow lake perturbed by episodic wind events. *Limnol. Oceanogr.* 35, 1050–1067. <https://doi.org/10.4319/lo.1990.35.5.1050>.
- Madsen-Østerby, M., Kragh, T., Pedersen, O., Sand-Jensen, K., 2018. Coupled UV-exposure and microbial decomposition improves measures of organic matter degradation and light models in humic lake. *Ecol. Eng.* <https://doi.org/10.1016/j.ecoleng.2018.04.01>.
- Middelboe, A.L., Markager, S., 1997. Depth limits and minimum light requirements of freshwater macrophytes. *Freshw. Biol.* 37, 553–568.
- Mitsch, W.J., Wu, X., Nairn, R.W., Weihe, P.E., Wang, N., Deal, R., Boucher, C.E., 1998. Creating and restoring wetlands. *Bioscience* <https://doi.org/10.2307/1313458>.
- Moreno-Mateos, D., Power, M.E., Comín, F.A., Yockteng, R., 2012. Structural and functional loss in restored wetland ecosystems. *PLoS Biol.* <https://doi.org/10.1371/journal.pbio.1001247>.
- Pant, H., Reddy, K., 2003. Potential internal loading of phosphorus in a wetland constructed in agricultural land. *Water Res.* [https://doi.org/10.1016/S0043-1354\(02\)00474-8](https://doi.org/10.1016/S0043-1354(02)00474-8).
- Pedersen, E.J., Miller, D.L., Simpson, G.L., Ross, N., 2019. Hierarchical generalized additive models in ecology: an introduction with mgcv. *PeerJ* 7, e6876. <https://doi.org/10.7717/peerj.6876>.
- Pérez, G., Lagomarsino, L., Zagarese, H.E., 2013. Optical properties of highly turbid shallow lakes with contrasting turbidity origins: the ecological and water management implications. *J. Environ. Manag.* <https://doi.org/10.1016/j.jenvman.2013.09.001>.
- R Core Team, 2021. *R: A Language and Environment for Statistical Computing (Manual)*. Vienna, Austria.
- Reardon, K.E., Bombardelli, F.A., Moreno-Casas, P.A., Rueda, F.J., Schladow, S.G., 2014. Wind-driven nearshore sediment resuspension in a deep lake during winter. *Water Resour. Res.* 50, 8826–8844. <https://doi.org/10.1002/2014WR015396>.
- Rooney, N., Kalf, J., 2000. Inter-annual variation in submerged macrophyte community biomass and distribution: the influence of temperature and lake morphometry. *Aquat. Bot.* [https://doi.org/10.1016/S0304-3770\(00\)00126-1](https://doi.org/10.1016/S0304-3770(00)00126-1).
- Sand-Jensen, K., 1998. Influence of submerged macrophytes on sediment composition and near-bed flow in lowland streams. *Freshw. Biol.* 39, 663–679. <https://doi.org/10.1046/j.1365-2427.1998.00316.x>.
- Sand-Jensen, K., Borum, J., 1991. Interactions among phytoplankton, periphyton, and macrophytes in temperate freshwaters and estuaries. *Aquat. Bot.* 41, 137–175. [https://doi.org/10.1016/0304-3770\(91\)90042-4](https://doi.org/10.1016/0304-3770(91)90042-4).
- Schallenberg, M., Burns, C.W., 2004. Effects of sediment resuspension on phytoplankton production: teasing apart the influences of light, nutrients and algal entrainment. *Freshw. Biol.* <https://doi.org/10.1046/j.1365-2426.2003.01172.x>.
- Scheffer, M., Hosper, S., Meijer, M., Moss, B., Jeppesen, E., 1993. Alternative equilibria in shallow lakes. *Trends Ecol. Evol.* 8, 275–279. [https://doi.org/10.1016/0169-5347\(93\)90254-m](https://doi.org/10.1016/0169-5347(93)90254-m).
- Simpson, G.L., 2018. Modelling palaeoecological time series using generalised additive models. *Front. Ecol. Evol.* 6, 149. <https://doi.org/10.3389/fevo.2018.00149>.
- Smith, R.C., Baker, K.S., 1978. Optical classification of natural waters. *Limnol. Oceanogr.* 23, 260–267. <https://doi.org/10.4319/lo.1978.23.2.0260>.
- Sø, J.S., Sand-Jensen, K., Baastrup-Spohr, L., 2020. Temporal development of biodiversity of macrophytes in newly established lakes. *Freshw. Biol.* 65, 379–389. <https://doi.org/10.1111/fwb.13431>.
- Sø, J.S., Sand-Jensen, K., Kragh, T., 2021. Optimal physical design in a new lake for reducing phosphorus pools. *Ecol. Eng.* 161, 106160. <https://doi.org/10.1016/j.ecoleng.2021.106160>.
- Søndergaard, M., Jensen, J.P., Jeppesen, E., 2003. Role of sediment and internal loading of phosphorus in shallow lakes. *Hydrobiologia* 506, 135–145. <https://doi.org/10.1023/b:hydr.0000008611.12704.dd>.
- Steinman, A.D., Ogdahl, M.E., 2011. Does converting agricultural fields to wetlands retain or release P? *J. N. Am. Benthol. Soc.* 30, 820–830.
- Valipour, R., Boegman, L., Bouffard, D., Rao, Y.R., 2017. Sediment resuspension mechanisms and their contributions to high-turbidity events in a large lake. *Limnol. Oceanogr.* 62, 1045–1065. <https://doi.org/10.1002/lno.10485>.
- van Dijk, G.M., Breukelaar, A., Gijlstra, R., 1992. Impact of light climate history on seasonal dynamics of a field population of *Potamogeton pectinatus* L. During a three year period (1986–1988). *Aquat. Bot.* 43, 17–41. https://doi.org/10.1007/978-94-011-2032-6_9.
- Wetzel, R.G., 2001. *Limnology: Lake and River Ecosystems*. Academic Press, Massachusetts.
- Whitmore, Thomas J., Brenner, M., Schelske, C.L., 1996. Highly variable sediment distribution in shallow, wind-stressed lakes: a case for sediment-mapping surveys in paleolimnological studies. *J. Paleolimnol.* 15, 207–221. <https://doi.org/10.1007/BF00213041>.
- Wine, M.L., Laronne, J.B., 2020. In water-limited landscapes, an Anthropocene exchange: trading lakes for irrigated agriculture. *Earth's Future* 8, e2019EF001274. <https://doi.org/10.1029/2019ef001274>.
- Wood, S.N., 2017. *Generalized Additive Models: An Introduction With R*. CRC Press, Florida.

- Yang, G., Moyer, D.L., 2020. Estimation of nonlinear water-quality trends in high-frequency monitoring data. *Sci. Total Environ.* 715, 136686. <https://doi.org/10.1016/j.scitotenv.2020.136686>.
- Zak, D., Goldhammer, T., Cabezas, A., Gelbrecht, J., Gurke, R., Wagner, C., Reuter, H., Augustin, J., Klimkowska, A., McInnes, R., 2018. Top soil removal reduces water pollution from phosphorus and dissolved organic matter and lowers methane emissions from rewetted peatlands. *J. Appl. Ecol.* 55, 311–320. <https://doi.org/10.1111/1365-2664.12931>.
- Zedler, J.B., Kercher, S., 2005. Wetland resources: status, trends, ecosystem services, and restorability. *Annu. Rev. Environ. Resour.* <https://doi.org/10.1146/annurev.energy.30.050504.144248>.