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Early ecosystem responses to watershed restoration along a headwater stream

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Abstract

Along many streams, natural riparian vegetation has been replaced by agricultural fields or plantations resulting in ecosystem alterations due to changes of the interactions across the land-water ecotone. We studied the effect of restoration interventions by removing a dense spruce plantation in a 25 m wide zone along a 4 km section of a headwater stream. Water discharge, nutrient and total organic carbon concentrations were unaffected by the intervention, which only involved 0.7 % of the catchment area. Focusing on the oxygen dynamics within several sections of the stream revealed that the stream water was generally oxygen under-saturated both before and after the restoration reflecting the dominance of heterotrophy over photoautotrophy typical of small streams. Oxygen saturation was tightly coupled to water discharge, with anoxia or hypoxia developing during low summer flow, and levels just below saturation during high autumn-spring flow at low temperature and low metabolism. Stream-near felling increased incident irradiance and reduced the duration and extent of summer hypoxia despite unaltered discharge, temperature and concentration of total organic carbon. Increased incident irradiance was accompanied by higher oxygen saturation in open sections compared to control sections with intact tree cover. Diel oxygen changes followed incident irradiance during low summer flow, while alterations at high winter flow were caused by changes in temperature-dependent oxygen solubility and high reaeration. In conclusion, we show that anoxic or hypoxic oxygen levels occur in warm, low-flow summer periods and this stress is reduced when intense shading from spruce plantation is removed and in-stream oxygen production is stimulated.

1 Introduction

Streams play a major role in global elemental cycles and exhibit high biodiversity, even though they occupy less than 0.6 % of the Earth's land surface (Downing et al., 2012; Strayer and Dudgeon, 2010). Small streams account for the main length of the world's lotic waters and because of intimate connection to the terrestrial environment, their ecosystem processes and biodiversity are strongly affected by riparian land use (Downing et al., 2012; Friberg, 1997). Changes from natural riparian zones to plantations, agricultural fields and urban areas have deteriorated environmental conditions along countless streams (see references in González et al., 2017). Knowledge on the ecological effects of these historical alterations as well as recent restoration attempts are few, but important for proper management to re-establish good ecological status of streams.

We investigated the effect of restoration interventions, in which Norway spruce (*Picea abies* (L) Karst.) plantations were cleared to allow natural secondary succession in a 25-m wide zone along a 4 km section of a headwater stream on the island of Bornholm, Denmark. Clearing of the spruce vegetation close to the stream will reduce the atmospheric input of needles and branches that normally reaches the stream (Iversen et al., 1982), but in contrast could increase the hydrological input of dissolved organic carbon and nutrients (Huber et al., 2004; Oni et al., 2015). We assume this influence on carbon input and mineral elements to the stream are minor because the felled area comprised only 0.7 % of the catchment area. We evaluated the influence by comparing stream transport before and after felling by calculating the potential change of input based on the size of the felled area. More importantly, felling the spruce trees along the stream may have an immediate and direct ecosystem effect by increasing light availability within the stream (Barbier et al., 2008). Alterations of the riparian zone vegetation may thereby influence stream water oxygen concentration by changing the balance between primary production, respiration and atmospheric gas exchange (Odum, 1956). Increasing incident irradiance by removing the forest canopy should increase primary production in the stream and may result in higher daytime oxygen concentration. However, it could potentially also lower nocturnal oxygen concentration caused by higher biomass of respiring phototrophic organisms and higher water temperatures enhancing respiratory rates and reducing oxygen solubility (O'Driscoll et al., 2016). Change in water discharge, and consequently water level and current velocity, because of altered catchment vegetation may also have a direct influence on oxygen pools and atmospheric gas exchange (Brown et al., 2005; Raymond et al., 2012).

Even though oxygen levels serve as a primary indicator of ecosystem processes, and is a key-factor for habitat suitability, few investigations have directly evaluated the effect of stream-near clearing on oxygen conditions (Bernot et al., 2010; Bunn et al., 1999; Clapcott and Barmuta, 2010; DaSilva et al., 2013; O'Driscoll et al., 2016). Here, we present comprehensive analyses of oxygen conditions and associated environmental variables from one year before to two years after clearing of the stream-near spruce plantations along a headwater stream. The overall objective was to elucidate the effect of restoring the natural stream-near vegetation on the stream ecosystem using oxygen condition as our sentinel, and to gain knowledge on the effect of stream-near plantation removal as a restoration tool. We aimed at understanding the temporal variation of oxygen and the influence of seasonal changes of incoming irradiance and water discharge. Our specific hypotheses were that: 1) increasing light availability by removing the spruce plantation would increase primary production in the stream leading to higher daily oxygen concentrations in well illuminated periods and stream reaches, 2) because of the very low proportion of felled area in the catchment, changes in hydrology and concentration and transport of nutrients and carbon would be insignificant, and 3) because of the small size of the stream, the effect of the restoration was subordinate to seasonal changes caused by changes in temperature and precipitation.

2 Materials and methods

2.1 Study site

The study was conducted along the uppermost 4 km of the stream 'Øle Å', Bornholm, Denmark (Figure 1). The stream originates from the protected wetland 'Ølene' and is unregulated, meandering through the rocky landscape with an average slope of 6.5 m km^{-1} in the study reach. The nearby area including the riparian zone has been managed as a plantation since the beginning of the 19th century primarily with Norway spruce *(Picia abies* (L) Karst.), which was planted close to the stream on approximately 56 % of the left stream bank and 54 % of the right stream bank of the study reach. Few wet riparian stretches were left with natural mixed deciduous forests or herb communities.

2.1.1 Restoration intervention

In autumn 2014, the dense spruce plantation was cleared in a 25 m wide belt along the stream (Figure 1). In total, spruce plantation was removed on 6.5 ha, corresponding to 0.7 % of the catchment area. The felling was made with minimum disturbance to the soil, particularly to the wet soils, the stream, and the existing natural vegetation. Tree stumps were left and a minimum of brash was allowed in the stream. After the intervention, the area was left to undergo secondary succession without any further intervention. In order to promote regrowth of deciduous trees, birch (*Betula* sp. L.), black alder (*Alnus glutinosa* Gaertn) and other native trees were left. In short sections along the stream one side of the stream bank was left un-cut, and at one 173 m long stretch both banks were left un-cut serving as a control (Figure 1).

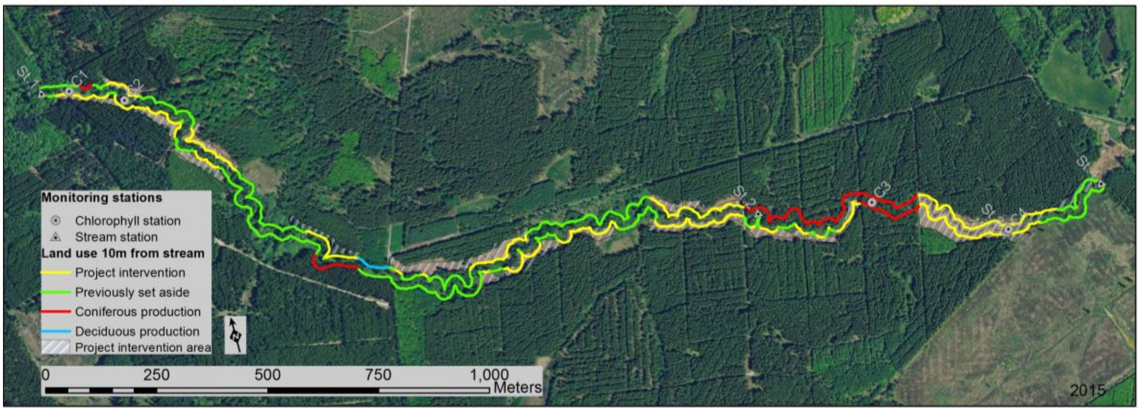

Figure 1: (TWO-COLUMN FITTING IMAGE, PRINT IN COLOR) *Aerial photo from 2015 of the area along the upper Øle Å. The areas felled are indicated by zones with white stripes. To illustrate the different forest and vegetation type along the stream a line was drawn along the stream 10 m from each stream bank and coloured according to land use. Yellow are areas felled as a restoration intervention; green indicate previously set aside areas; red are control areas, where the spruce plantation is left intact; blue are areas with deciduous forest. Monitoring stations (St.) and chlorophyll sampling stations (C) are shown with grey triangles and dots, respectively. © COWI DDOland 2015.*

2.2 Monitoring stations

To ensure a proper coverage of the variability of environmental conditions and to evaluate the restoration effects, four monitoring stations were set up along the study reach (Figure 1). Station 1 was located in mixed forest just upstream of the cleared areas. Station 2 was set in an area approximately halfway through the study reach, with intervened areas until about 50 m upstream. Station 3 was located in an entirely cleared area close to the end of the study reach. Station 4 was located at the end of the study reach in a mostly open area with a mixture of deciduous trees and spruce. Stations 1, 2, and 4 were monitored from 2013 to 2016, whereas Station 3 was added as a supplement for campaigns, 7 days in June 2015, from December 15, 2015 to January 12, 2016 and from the March 8 to May 12, 2016.

2.2.1 Oxygen and temperature

Oxygen concentration and water temperature were measured at 10 minutes intervals at the stations using oxygen sensors (MiniDOT logger, Precision Measurement Engineering, Inc., Vista, Ca, USA). Before and after deployments, oxygen sensors were calibrated in 100 % oxygen-saturated water bubbled with atmospheric air and 0 % oxygen saturated water bubbled with nitrogen. Oxygen concentrations were corrected for drift (maximum 2 %) during deployment assuming linear changes over time. Freezing during cold winter periods prevented proper sensor functioning and sensors were withdrawn from the stream until suitable conditions resumed.

2.2.2 Hydrodynamics

Water level at Station 1, 2, and 4 was measured every 15 minutes from May 2013 and onwards by recording pressure differences between a submerged water level data logger (HOBO U 20 – 001-04, Onset Computers, Bourne, USA) and a similar logger in air. Water depth was validated by manual measurements.

Continuous water discharge was calculated for station 4 based on continuous water level recordings and a long-standing Q-H relation (Poulsen and Ovesen, 2011). To estimate discharge at stations 1 and 2, we applied corrections for watershed size.

2.2.3 Light

Light loggers (HOBO Logger UA-002-64, Onset Computer, Bourne, Massachusetts, USA) were placed at every station next to the stream. At Station 2 the logger was placed about 150 m upstream the monitoring station in a cleared area with only few deciduous trees present close to the stream. Light intensity (LUX) was measured every 5 minutes. In addition, a permanent weather station located in a large clear-cut 50 m from Øle Å measured incident photon flux density (PAR, 400-700 nm; Photosynthetic Light (PAR) Smart Sensor, Onset Computer, Bourne, Massachusetts, USA).

2.2.4 Benthic algal biomass

At four separate stations (C1-C4, Figure 1), benthic algal biomass was measured as chlorophyll *a*. Station C1 was located at a partly open reach in the upper part of the study reach, with just minor intervention. At C2 trees had been removed. Station C3 was located at the control stretch without clearing, while C4 was located at a fully cleared site. Samples were collected two to four times a year from 2014 to 2016.

At each station three stones (3-6 cm in diameter) and one sediment sample (4.91 cm^2 of the sediment surface and 10 cm^3 of sediment volume) were randomly collected in triplicates. The stones and sand were covered with 96 % ethanol and chlorophyll was extracted for 24 hours at room temperature in darkness, filtered through 47 mm GF/C filters and absorbance measured in a spectrophotometer (UV-1800, Shimadzu, Japan) at 665 nm and 750 nm (Jespersen and Christoffersen, 1987). Stone surface area was measured using ImageJ 1.46r (Wayne Rasband, National Institutes of Health, Maryland, USA).

2.2.5 Nutrients and organic carbon

Water samples were collected at Stations 1, 2 and 4 every 15 days from summer 2013 to 2016. Samples for analysis of nitrogen (ammonium and nitrate) and phosphorous (orthophosphate) were frozen at -18^o C immediately after returning from the field. Nitrate, ammonium and phosphate were analysed on thawed and filtered water samples using an Alpkem autoanalyzer and an UV spectrophotometer (UV-1800, Shimadzu, Japan). Total organic carbon (TOC) was analysed on unfiltered 15 ml water collected at the same stations and time intervals as nutrient analyses. Immediately after collection, TOC samples were conserved with 150 µl 2 M HCL and stored in darkness until analysis on an organic carbon analyser (TOC-V CPH, Shimadzu, Japan) following methods in Kragh and Søndergaard (2004).

Transport of nutrients and TOC was calculated by multiplying water discharge with concentrations. Input of TOC along the 4 km long stream reach was evaluated by comparing transport at the upstream and downstream stations (St. 1 and 4), Moreover, potential influence of felling was evaluated by comparing the potential decrease of annual allochthonous carbon input and increase of seepage water based DOC input from the felled area with measured downstream TOC transport.

2.3 Statistical analyses

Differences in oxygen saturation measured every 10 minutes at station 2 and 3 during summer and spring, was tested by a Wilcoxon paired t-test performed for the periods 22-28 June 2015 and 15-28 April 2016. These time periods were selected as they were the only periods with data from both a clear cut (Station 3) and a partly closed canopy stream reach (Station 2).

To test if there was a difference in the relation between water depth and oxygen saturation before and after the intervention an ANCOVA was performed on oxygen saturations below 90 % and depths below 31 cm. The analysis was based on values of daily mean water depth (cm) and oxygen saturation (%) from 2013 to 2016.

The effect of clearing on light availability at the stream surface was analysed using linear regressions of unshaded-PAR versus stream-surface-LUX for each station before and after felling using daily mean values from August 2013 to September 2016. The slope of the regression models before and after forest clearance was used to calculate the proportional change in incident light at each station. Slope differences of the linear regressions before and after felling were tested by ANCOVA.

The weekly mean water temperature for the months April-August before and after felling was analysed with a paired t-test to test if clearance affected stream temperature. Prior to performing the paired t-test a Shapiro Wilks-test was carried out in order to ensure a gaussian distribution of the residuals.

A two-way ANOVA followed by Sidak's multiple comparison test was used to test for difference in chlorophyll *a* concentration as a function of time and location, by comparing every chlorophyll *a* measurement at Station C1, C2, C3 and C4.

All statistical analyses were carried out using GraphPad Prism v. 6.0.

3 Results

3.1 Oxygen dynamics and hydrodynamic impact

The stream water was usually under-saturated in oxygen relative to the atmosphere at all three permanent stations (Station 1, 2 and 4) (Figure 2). The oxygen saturation fluctuated across seasons with oxygen saturation reaching 0 % during summer and being close to 100 % during winter.

Discharge played a key role for the oxygen saturation with conditions varying from almost stagnant, shallow water during summer to fast running deeper water during winter (Figure 3).

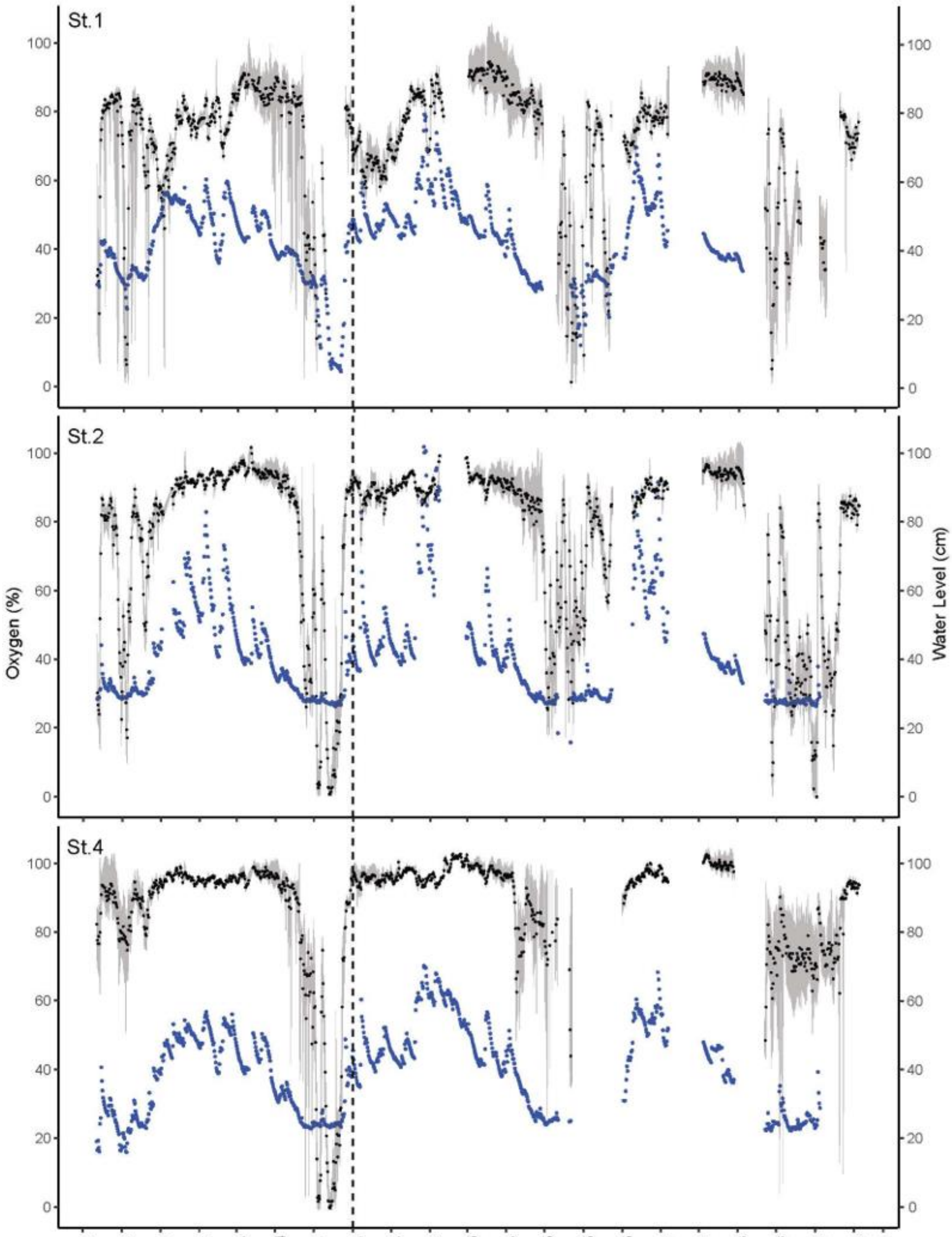

Figure 2: (TWO-COLUMN FITTING IMAGE, PRINT IN COLOR) *Daily mean of oxygen saturation (%) at Station 1, 2 and 4 for the entire sampling period. Black dots show mean oxygen saturation (%), grey area shows the range*

between min- and max-saturation for each day, and blue dots represent the daily mean water level. The vertical dashed line represents the time of felling.

At low water level both low and high oxygen saturation occurred, while high water levels were accompanied by oxygen levels close to air saturation (Figure 3). Low oxygen saturation was restricted to periods of low discharge (Figure 3).

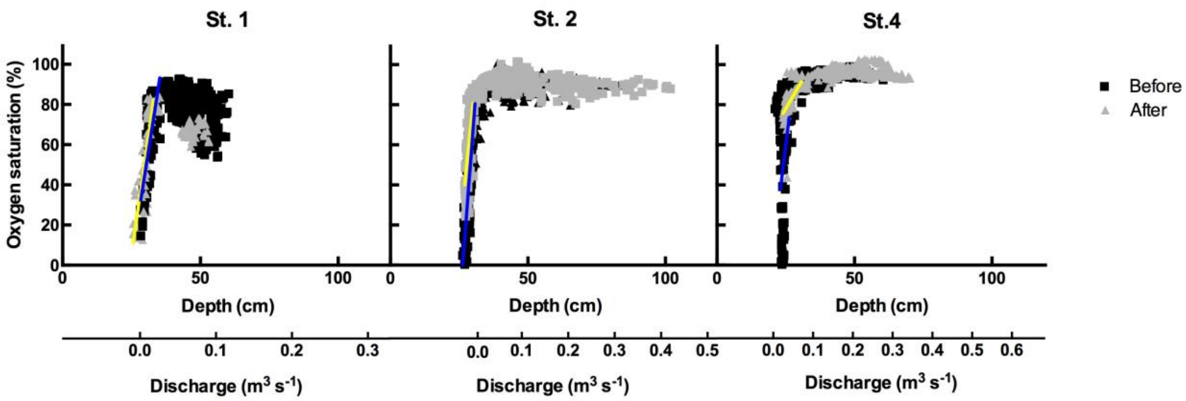

Figure 3: (TWO—COLUMN FITTING IMAGE, PRINT IN COLOR) *Daily mean oxygen saturation (%) was related to daily mean water level (cm) and mean discharge ($m^3 s^{-1}$) for each station from 2013 to 2015 in low flow periods. Black squares represent data from before the intervention while grey triangles represent data from after the intervention. The blue and yellow regression lines show the relation between depth (<31 cm) and oxygen saturation (<90 %) before and after the intervention respectively. ANCOVA analysis showed that the regression lines at Station 2 and 4 were significantly different (p=0.015 and p=0.023, respectively), while they were not different at Station 1 (p=0.53).*

3.2 Changes in oxygen saturation after the intervention

At the two permanent stations with partly cleared reaches (Stations 2 and 4, Figure 1), the daily mean oxygen saturation increased during summer at low or stagnant flow after the intervention compared to Station 1 where no clearing had taken place (Figure 2). In 2016, almost two years after the intervention, oxygen concentrations at Station 4 showed higher minimum levels compared to before the intervention (Figure 2).

Also, the relationship between water level and oxygen saturation changed significantly at Station 2 and 4 (ANCOVA, p=0.015 and p=0.023, respectively). The two stations, however, did not respond similarly to the changes. At Station 2, the relationship between water level and oxygen became steeper, indicating that oxygen declined at a lower water level after forest clearing than before. At Station 4, periods with low oxygen saturation did not occur after the restoration (minimum daily mean oxygen saturation was 44 %) resulting in a more gradual slope between oxygen saturation and water level. At Station 1, where no intervention had taken place, there was no significant changes in the relation between water level and oxygen saturation in the years before and after the intervention (ANCOVA, p>0.5; Figure 3).

3.2.1 Spruce shading and oxygen saturation

The cleared reach (Station 3) and the partly cleared reach (Station 2) downstream the intervened areas differed significantly in mean oxygen saturation and diel fluctuations during summer 2015 (paired t-test, $p \leq 0.0001$; Figure 4B). The cleared reach was having the highest oxygen concentrations. The difference in saturation between the two sites was highest in the late afternoon (max 22 %) and lowest at night. Oxygen saturation exceeded 100 % every day at the cleared reach, while it stayed below atmospheric saturation at the partly cleared reach (Figure 4B). Also during spring, the oxygen saturation at the cleared reach was significantly higher compared with the partly cleared reach (paired t-test, $p \leq 0.0001$), although the absolute differences were small (max 7 % saturation).

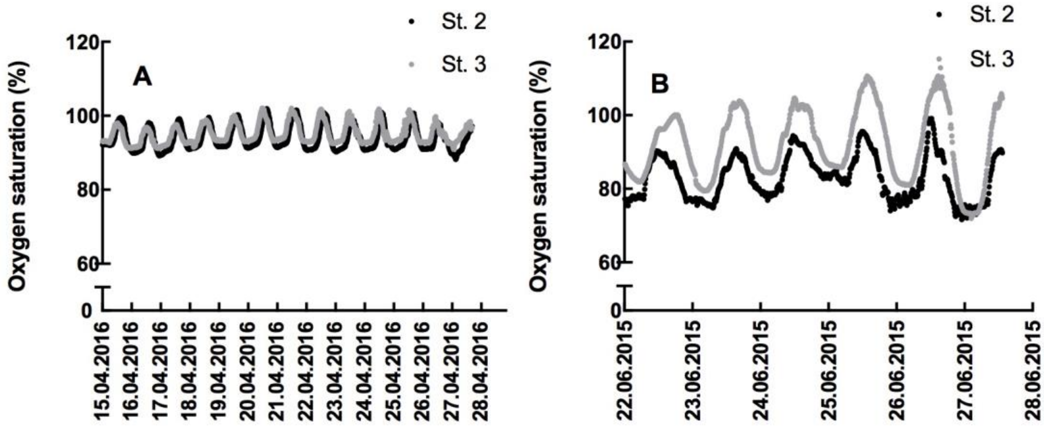

Figure 4: (TWO-COLUMN FITTING IMAGE) *Oxygen saturation at Station 2 (control with spruce plantation) (black circles) and Station 3 (cleared area; grey circles) during A) 14 days in April 2016 and B) five days in June 2015.*

3.3 Temperature and light

Water temperature (weekly averages) varied with season, having lower temperature during winter and higher during summer. The average weekly temperature from April to August for each permanent station did not differ significantly in response to the intervention (paired t-test, $p>0.05$).

Light intensity reaching the stream followed the same seasonal pattern as above the canopy. However, before the felling the light flux reaching the stream was strongly dampened (Figure 5). After clearing, the mean daily incoming light increased markedly at Station 2 (7-fold) and Station 3 (15-fold). To test if these changes were due to altered cloud cover between years, stream level LUX was compared to above-canopy PAR. The slope of the relationship was significantly steeper after the intervention at Station 2 and 3 (ANCOVA, $p\leq0.001$, Figure 5) confirming that a 7-15-fold higher proportion of incoming light reached the stream after the intervention. After the intervention, the relationship between above-canopy PAR and light reaching the stream had larger residuals at Station 2 compared to Station 1, owing to shading from solitary birch trees left uncut as part of the restoration.

At Station 1 (where no felling took place) there was a relatively small but significant reduction in the amount of light reaching the stream compared to above canopy measurements (ANCOVA, p=0.002).

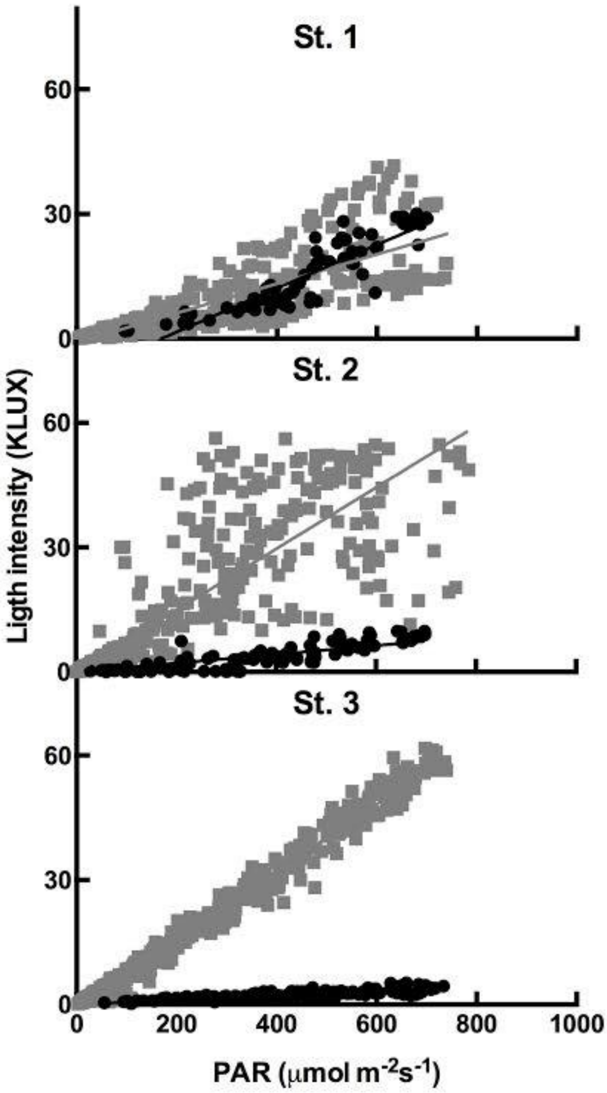

Figure 5: (SINGLE-COLUMN FITTING IMAGE) *The relationship between lumen influx per m^2 (LUX) at the stream surface for each station and the photosynthetically active radiation (PAR) measured at the weather station. Black circles are before the intervention and grey squares after the intervention.*

3.4 Algal biomass

There were no significant annual changes in the benthic algal biomass during summer and autumn as a response to the intervention. However, the biomass on sand tended to be higher during summer at the most open station (C4) after felling (Figure 6).

Also, at C4 massive growth of filamentous green algae (*Cladophera sp.)* was observed in spring and summer 2015, but not in 2014. None of the other stations in any of the years showed growth of filamentous algae.

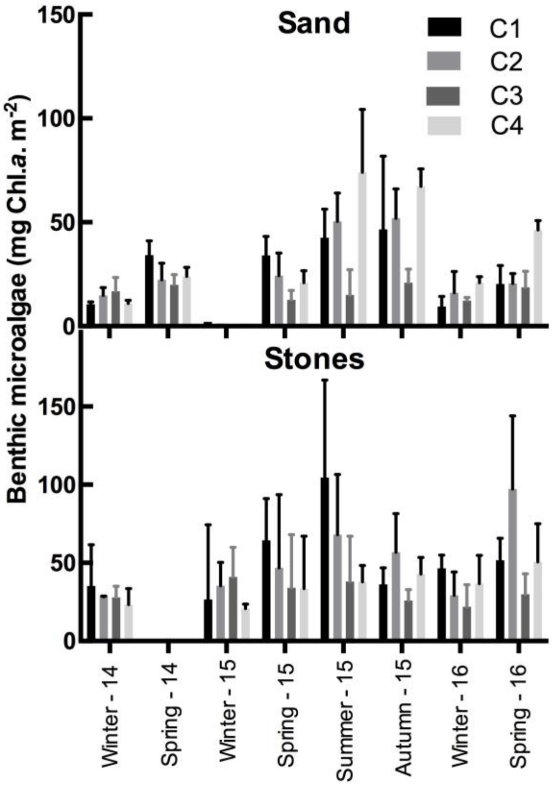

Figure 6: (SINGLE-COLUMN FITTING IMAGE) *Mean chlorophyll a concentration on sand and stones (mg Chl. a m^{-2}) from winter 2014 to spring 2016. Standard deviations are shown by error bars.*

Comparing the winter biomass of benthic algae before and after the intervention on sand and stones showed no differences (two-way ANOVA, p>0.05), except for the significantly higher winter and spring levels in 2016 than in 2015 on sand at Station C4 (two-way ANOVA, $p \leq 0.0001$ and $p \leq 0.01$).

3.5 Nutrients and organic carbon

Concentrations of nitrate, ammonium and phosphate were generally low (Figure 7). Nitrate and to some extent ammonium varied seasonally, whereas phosphate did not. For N and P, the concentrations generally declined from the upstream Station 1 towards the lower Stations 2 and 3 (Figure 7). The temporal patterns of nutrient concentrations were the same before and after the felling and, thus, there were no indications that the clearing influenced the concentrations or the pattern of declining concentrations along the studied reaches.

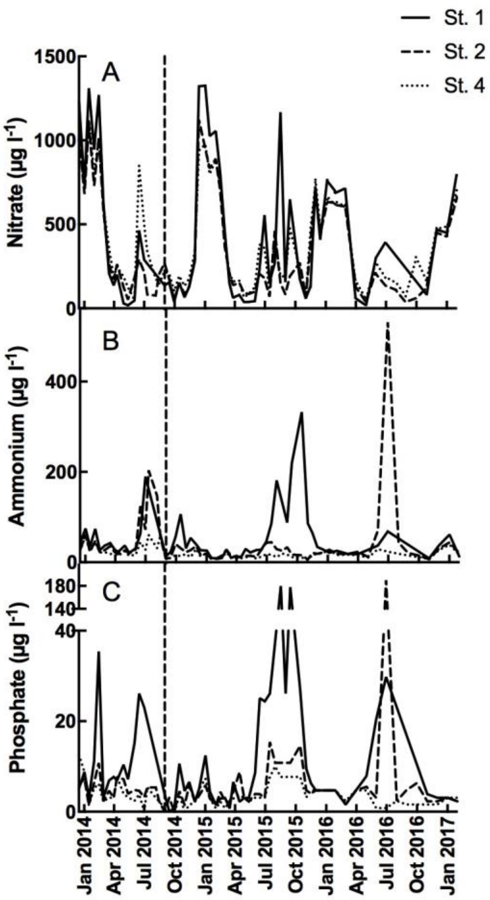

Figure 7: (SINGLE-COLUMN FITTING IMAGE) *Concentrations (µg l^{-1}) of nitrate, ammonium and phosphate at Station 1 (solid line), Station 2 (dashed line) and Station 4 (dotted line over three years. The time of felling is shown by the stippled vertical line.*

Concentrations of TOC varied seasonally showing the highest values in the autumn and the lowest during spring and summer (Figure 8A). Throughout the surveyed period the concentrations in the inlet (St. 1) and outlet (St. 4) of the investigated reach trailed each other closely, though in the summer of 2015 concentrations were somewhat higher at the inlet compared with the outlet (Figure 8A). TOC transport was very similar at the inlet and outlet stations (Figure 8B) and annual TOC transport at the outlet station amounted to 16.9-28.6 ton C year^{-1} in the three years.

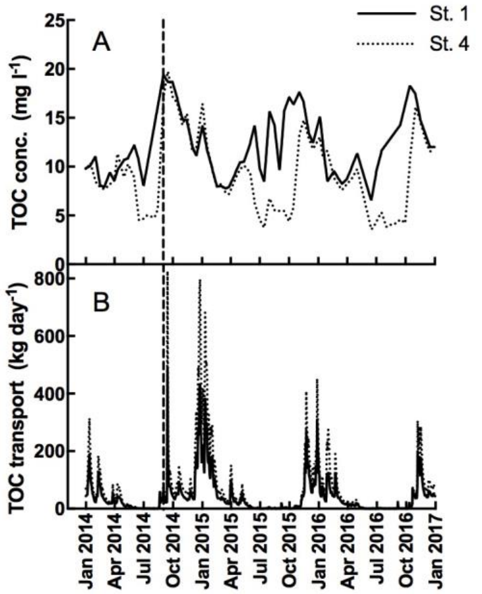

Figure 8: (SINGLE-COLUMN FITTING IMAGE) *A): TOC concentrations (mg L$^{-1^1}$) at Stations 1 and 4 over three years. B): TOC transport (kg day^{-1}) at Stations 1 and 4. The time of felling is marked by the stippled vertical line.*

Mass balance evaluations supported that felling along the stream, amounting to only 0.7 % of the catchment area, had a small influence on TOC transport. Annual litterfall of TOC from Norway Spruce in Denmark is typically 0.13 kg C m^{-2} (Hansen et al., 2009). Felling occurred along 666 m of the 2.3 m wide stream. Thus, the annual direct input to the stream surface is reduced by about 666 * 2.3 * 0.13 = 190 kg organic C. DOC concentrations in water runoff from Norway spruce areas, which has been clear cut or naturally died back, have been reported to increase by 1 mg C L^{-1} in mid-Sweden (Oni et al., 2015) and 3.6 mg C L^{-1} in Germany (Kopáček et al., 2017). Other authors have reported a 50 % increase of DOC concentrations after felling, which is equivalent to about 5 mg C L^{-1} in Øle Å. With an annual runoff of 170 - 270 L m^{-2} from the felled area in the investigated period, the estimated increase of annual DOC input is in the range of 1-5 g C m^{-2}, or 10-85 kg C for the entire felled area. Both the potential decrease of macroscopic plant litter and the increase of dissolved matter from the felled area to the stream were much lower than transport at the downstream station in accordance with the non-significant change in TOC transport from before to after felling.

4 Discussion

4.1 Seasonal oxygen dynamics

In evaluations of suitable and critical conditions for the stream biota it is essential to know the environmental conditions at high temporal resolution through different seasons and several years. In the case of fish and macroinvertebrates with long generation times, long-term records of oxygen conditions are particularly relevant for evaluation of their population development. Short periods with poor conditions are sufficient to have a negative impact on fish and macroinvertebrate communities. In small temperate streams, oxygen saturation could be expected to decrease at low flow during summer and be closer to air saturation at high flow during autumn, winter and spring (Hornbach et al., 2015). In Øle Å, oxygen saturation varied greatly from hypoxic values (< 20 % air saturation) during summer days every year to permanently high oxygen saturation (> 90 % air saturation). The seasonal variations in oxygen saturation levels and hypoxic episodes during summer are more extreme than what is observed in most streams having more constant oxygen concentrations closer to air saturation throughout the year (Brisbois et al., 2008; Hornbach et al., 2015; Soulsby et al., 2009).

Oxygen saturation in Øle Å was highly dependent on the variable discharge. This is due to a relative thin soil-layer covering the bedrock in the watershed and, thus a small input of groundwater that may buffer discharge. At all three monitoring stations, oxygen concentrations decreased when discharge declined. The dependency of oxygen concentration on discharge and the coupled current velocity resulted, as already emphasized, in very low summer oxygen concentrations and detrimental effects on brown trout (*Salmo trutta*), which experienced higher mortality (Baastrup-Spohr et al., 2015; Ice and Sugden, 2003).

When water discharge is low and current velocity approaches zero, reaeration is markedly reduced (Kallenbach, 2016). Also, at low water level, water has a longer contact time with the sediment and the small oxygen pool is consumed. In addition, when water levels are low during summer, water temperature increases and oxygen solubility declines.

4.2 Effects of the intervention on oxygen

Clearing of the spruce plantation in the riparian zone increased light availability and reduced hypoxic events in Øle Å during summer due to higher oxygen production by photosynthesis. Because the minimum water level, and thereby the lowest discharge, was at the same level in summer 2014, 2015 and 2016, altered discharge cannot account for the higher minimum level of oxygen saturation at the three intervened stations.

While we found a positive effect on oxygen saturation levels by felling the stream-near spruce trees, as hypothesized, Moring and Lantz (1975) found a negative effect of logging, with oxygen concentration decreasing from 6-13 mg l^{-1} to 2 mg l^{-1}. In their study, the reduced oxygen concentration persisted until brash was removed from the stream. Another study found a reduction in oxygen concentration from 6.4 to 0 mg l^{-1} after forest clearance in the riparian zone of a stream (Plamondon et al., 1982). However, in this study, brash was not fully removed from the stream and could exert a substantial oxygen consumption. In Øle Å, woody brash from the intervention was avoided as far as possible in the stream, though inevitable. The degradability of spruce wood and needles is generally low (Lidman et al., 2017) and the observed difference between our investigation and other studies is therefore most likely caused by a combination of the small amounts and low degradability of the brash left after the intervention along Øle Å.

Due to the tight coupling between water discharge and oxygen saturation in Øle Å, it was examined whether this relationship changed in response to the intervention. Our results showed significant changes at both Station 2 and 4, whereas no change was found at Station 1 upstream the intervention. The increased slope of the regression for Station 2 indicated that oxygen saturation continued to be high at lower water levels after the intervention. At Station 4, the slope decreased, which indicates the absence of hypoxic events after the intervention.

No effect of the intervention was found on temperature, nitrogen, phosphorus and total organic carbon (TOC) concentrations. Earlier studies have shown an increase in stream water TOC concentrations and transport following forest felling and attributed these changes to increased leaching (Huber et al., 2004; Kopáček et al., 2017; Oni et al., 2015). However, in the current investigation the area felled was too small to cause a measurable effect on concentrations and transport in the stream. Simple mass balance calculations based on standard levels of atmospheric and hydrological TOC inputs from established and felled Norway spruce forest supported the direct measurements.

Despite the large decrease of input of needles and spruce wood debris to the stream following the intervention did not have a measurable influence on allochthonous TOC transport and oxygen levels in the stream, it might influence the macroinvertebrate fauna temporally reducing a food source (needles) and habitat structuring elements (large woody debris). Needles however, represent a poor food source compared with leaves of herbs and most deciduous trees (Webster and Benfield, 1986) and it is likely that regrowth in the felled areas would over time change the macroinvertebrate community because of altered allochthonous inputs.

The non-significant influence of felling on hydrology, nutrients and TOC in Øle Å leaves increased incident light on the stream as the only important factor explaining the increased oxygen levels during summer. This conclusion was supported by comparing Station 2 and 3 in June 2015. Here, oxygen saturation was evidentially higher in the fully open stream reaches than in the partly shaded reaches. The daytime amplitude of oxygen fluctuations was also higher at Station 3 in the completely cleared reach (70-112 % saturation) compared to Station 2 in the control reach (70-100 %). During night-time, the difference between Station 2 and 3 (0-3 % saturation) was negligible.

Considering the future development of Øle Å, we expect that the intervened areas will experience regrowth and establish a mixed deciduous forest, as already seen in previously set aside areas. This will reduce the amount of incoming light during the summer months of low flow. During spring months before foliation, however, light will reach the stream and stimulate photosynthesis and growth of benthic algae and plants. Beside the effects on light availability and in-stream oxygen production, a deciduous forest will lead to increased allochthonous input of easily degradable material, which can stimulate occurrence of macroinvertebrate shredders as well as whole-stream respiration and perhaps reduce the nighttime oxygen content.

4.3 Effects of forest clearance on benthic biomass

Benthic algal biomass was measured as a proxy for primary production, as benthic algae are the dominant primary producers within a stream. Algal biomass on sand and stones was expected to increase at the cleared stretches, as a response to the increased light availability (Sand-Jensen et al., 1998). Indeed, benthic biomass on sand at the different stations suggested a positive effect of the intervention, though the comparison suffered from high variability among replicates. The algal biomass on stones did not respond significantly to the intervention, whereas an increase was seen on sand at Station 4 in winter and spring from 2015 to 2016. The increase of oxygen concentrations at the open reaches is most likely due to increased photosynthesis of benthic algae owing to better light availability, though the algal biomass response was limited, perhaps because invertebrate grazers could keep down the algal biomass (Kjeldsen et al., 1998). Studies on the metabolism in Øle Å, did indeed reveal a higher gross primary production after the intervention at Station 2 and 4 compared with Station 1 (Kallenbach, 2016). This indicates that the stream before the intervention was light limited. The lack of effect on the benthic biomass could also be influenced by structural changes in the grazing community (Kjeldsen et al., 1998).

5 Conclusion

The high frequency measurements of oxygen and water level proved Øle Å to be net heterotrophic and have a highly dynamic hydrologic regime. There was a close relationship between oxygen concentration and water discharge, with oxygen saturation approaching zero at low discharge. The removal of spruce plantations in the riparian zone increased oxygen concentrations in the summer and reduced the detrimental effect of low water discharge leading to fewer and less hypoxic episodes. The restoration intervention along Øle Å thereby improved oxygen conditions for fish and animals within the stream. The observed effects were likely due to increased light availability, the only environmental factor showing significant changes following felling along the stream banks.

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