

# Annual changes in aquatic plant photosynthesis in the regulated river Otra and the effect of plant removal



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**Summary**

Mass development of submerged aquatic plants is often seen as nuisance for human activities. The present study used novel methods to estimate the changes in ecosystem photosynthesis (mostly *Juncus bulbosus*), through an annual cycle, under varying dissolved gas supersaturation events in the Rysstad basin, Otra River. The methods and results from this study may help us to understand the dynamics between supersaturation, *J. bulbosus* and fish health, and guide management decisions on aquatic plant removal.

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## Preface

All authors were involved in discussions to design the study. Sebastian Stranzl and Benoît Demars were responsible for deploying sensors. Kirstine Thiemer, Susanne Schneider and Benoît Demars collected and prepared the water samples for gas chromatography. Peter Dörsch analysed the samples by gas chromatography. Devanshi Pathak and Benoît Demars developed a novel model to estimate stream photosynthesis and respiration. Peter Dörsch and Benoît Demars developed a novel method to estimate photosynthesis and respiration under gas supersaturation from the hydropower plant. Benoît Demars ran the calculations and drafted the report.

We thank Gjermund Espetveit (Otra Kraft) and Ole Morten Egeland (Agder Energy) for providing flow data; Torstein Try for providing the boats; Odd Arne Skogan for setting up the Campbell logging station at Straume; Leonhard B. Jansen for changing and recharging the batteries of the logging station at Straume; Knut Olav Oppstad for providing sonar bathymetric data; Emmanuel Bergan, Astrid Torske, Eirin Aasland for help collecting water samples, bathymetric and plant data, as well as CO<sub>2</sub> flux with the floating chambers. Laurence Carvalho commented on the report.

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Oslo, 27.04.2023

*Benoît O.L. Demars*

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# Summary

## Introduction

The regulation of river flow to produce electricity may promote the mass development of submerged aquatic plants, often seen as nuisance for human activities, such as boating, swimming, fishing and hydrology of the system. Undesirable plant growth leads to costly remedial actions with variable effectiveness. Proliferation of plants can alter aquatic biodiversity and ecosystem functioning. Aquatic plants are often removed mechanically. Knowledge of plant growth rate and its main drivers could help management decide on plant removal because it would enable better estimates of regrowth.

The River Otra is situated in southern Norway and flows through alpine landscapes and forests. The River Otra is extensively regulated for hydropower. The studied section drains about 1900 km<sup>2</sup>, mostly through Brokke hydropower plant, and discharge is heavily regulated with characteristic diel changes (hydropowering) to accommodate demand in electricity. The hydropower plant periodically discharges water highly supersaturated in total dissolved gases (TDG) due to air entrainment in the water intakes. Fish and invertebrates that respire in supersaturated water may develop gas bubble disease (analogous to the bends in humans), with subacute mortality from about 110 % TDG in Atlantic salmon (*Salmo salar*).

Mass development of the submerged aquatic plant *Juncus bulbosus* (L.) in the Rysstad basin about 3-7 km downstream of Brokke is limiting human activities, such as boating and angling. Drifting plant material may also clog the inlet of the downstream hydropower plant Hekni. Dissolved CO<sub>2</sub> may potentially be a limiting factor for photosynthesis in Otra based on in-situ concentrations and published laboratory experiments. An increase in dissolved CO<sub>2</sub> during supersaturation events may potentially boost aquatic plant photosynthesis, which in turn may exacerbate total dissolved gas supersaturation during the day, due to slower gas exchange rate with the atmosphere for dissolved O<sub>2</sub> than dissolved CO<sub>2</sub>.

The present study used novel methods to estimate the changes in photosynthesis through diel studies over a year under varying TDG saturation in the Rysstad basin. Predictive models of plant photosynthesis based on temperature and light availability were used to generalise the findings and explore the effect of mechanical plant removal with varying degree of plant cover removal. More specifically, we aimed to resolve three questions:

1. Can TDG supersaturation events from Brokke hydropower plant increase dissolved CO<sub>2</sub> and boost aquatic plant photosynthesis?
2. Can aquatic plant photosynthesis increase TDG supersaturation in the water, thereby increasing risk to fish health?
3. How fast will *J. bulbosus* grow following mechanical removal?

## Methods

Water samples were collected to determine dissolved gases (O<sub>2</sub>, argon, CO<sub>2</sub>), at the entrance (Rysstad) and downstream end (Straume) of the Rysstad basin every two-hours for 24 hours on the 12-13 and 25-26 June 2020, during events with high levels of supersaturation (TDG>140% at the outlet of the hydropower station). We developed a novel method based on the relationship between O<sub>2</sub> and argon to partition changes in dissolved O<sub>2</sub> due to physical processes (hydropower plant dissolved gas supersaturation) and biological processes (photosynthesis and respiration). We

compared these results with measurements made in August 2019 during a period with low TDG supersaturation.

We installed a monitoring station at the downstream end of the Rysstad basin to estimate and predict changes in photosynthesis throughout the year. The station logged dissolved O<sub>2</sub>, temperature and light every 15 min from 25 November 2019 to 26 November 2020. An additional O<sub>2</sub> sensor was deployed at the inlet of the Rysstad basin. We also monitored TDG in the outlet of the Brokke hydropower plant. Data on river discharge were provided by the hydropower company (Otra Kraft). We estimated daily aquatic photosynthesis with a novel model based on a mass balance of O<sub>2</sub>.

Finally, we combined a predictive model for aquatic plant photosynthesis with published experimental data from Mandalselva to explore how plant mass development and photosynthesis may be affected by mechanical plant removal over a four-year period. We tested the model with on-going monitoring of vegetation in the Rysstad basin before and after mechanical plant removal in June 2020.

### Results and discussion

We found that the concentrations of CO<sub>2</sub> at the entrance (Rysstad) and outlet (Straume) of the Rysstad basin were similar, independently of TDG supersaturation (range 105-180%) at the outlet of the hydropower plant. We did not observe a boost in aquatic plant photosynthesis, likely because the CO<sub>2</sub> concentrations were more controlled by ecosystem metabolism (respiration and photosynthesis). If anything, *J. bulbosus* photosynthesis was slightly higher in August 2019 under low TDG saturation (105-110%) than in June 2020 under high TDG saturation (140-180%). **Thus, photosynthesis was not related to CO<sub>2</sub> and TDG saturation and we concluded that TDG saturation from the Brokke hydropower plant will likely not boost the photosynthesis of *J. bulbosus*.** In fact, a recent study suggested that aquatic plants may reduce TDG in the water column by increasing the rate of bubble formation over their surface and boost the gas evasion rate to the atmosphere.

Demars et al. (2021) concluded that aquatic plant photosynthesis in the Rysstad basin may increase the TDG supersaturation by up to 5%. This estimate was based on the differing gas exchange rate of CO<sub>2</sub> and O<sub>2</sub> at the water-air interface. However, aquatic photosynthesis was orders of magnitude larger than gas exchange rates in the Rysstad basin and about 80% of the oxygen produced was compensated by CO<sub>2</sub> uptake. **Thus, photosynthesis will likely not increase TDG by more than 1% at the surface water. This increase poses virtually no further risk to fish health,** especially since trout in Rysstad prefer deeper parts of the river where hydrostatic pressure will reduce the TDG supersaturation.

The annual monitoring of oxygen concentrations and the application of a new model revealed that photosynthesis of *J. bulbosus* was related to light availability and temperature. Photosynthesis was lowest during the winter due to light and temperature limitations. Photosynthesis remained low until the end of May due to cold temperature. In June, photosynthesis increased sharply with temperature, stayed relatively high until September, and then declined with temperature and light to the winter minimum. ***J. bulbosus* was able to perform photosynthesis year-round, including during the winter months. Photosynthesis will likely occur to a smaller extent in unregulated rivers due to lower temperatures and ice cover.**

We estimated that the annual gross primary production (GPP) in the Rysstad basin is 271 g C m<sup>-2</sup> year<sup>-1</sup>. If we assume that 50% (range 20-80%) of GPP is used by the plants during respiration, then the net primary production (i.e., the carbon stored as biomass) will be 135 (54-217) g C m<sup>-2</sup> year<sup>-1</sup>. **The annual growth of *J. bulbosus* is therefore 2.4 (1.0-3.8) times larger than the average standing**

**biomass in the Rysstad basin (circa  $57\pm 8$  g C m<sup>-2</sup>). Thus, large amounts of plant mass are likely lost through hydraulic stress and natural mechanical breakage of stems.** This matches personal observations of drifting *J. bulbosus* at virtually any time of the year.

Our model indicated that the photosynthesis of *J. bulbosus* would recover rapidly (likely within two years) after 50-85% removal of the plant. If 99% removal could be achieved, *J. bulbosus* would remain below 50% of its capacity after three years. **On-going monitoring of vegetation in the Rysstad basin confirmed that *J. bulbosus* recovered within two years following mechanical removal in June 2020 of  $72\pm 17$  % biomass or  $84\pm 6$ % biovolume ( $\pm$ se).**

### **Conclusion**

Supersaturation events did not increase CO<sub>2</sub> availability and photosynthesis of *J. bulbosus* in the Rysstad basin. A lack of plant boost was likely due to rapid degassing of CO<sub>2</sub> upstream the Rysstad basin, and dissolved CO<sub>2</sub> concentrations were likely more controlled by in-stream metabolism. Photosynthesis of *J. bulbosus* did likely not pose any further risk to fish health from increased O<sub>2</sub> that adds to the total dissolved gas supersaturation. The regrowth of *J. bulbosus* may be slowed if a very high efficiency of plant removal can be achieved. The methods and results from this study may help us to understand the dynamics between supersaturation, *J. bulbosus* and fish health, and guide management decisions on aquatic plant removal.



# Sammendrag

Tittel: Årlige endringer i vannplanters fotosyntese i den regulerte elven Otra og effekten av plantefjerning

År: 2023

Forfatter(e): Benoît O.L. Demars, Susanne C. Schneider, Kirstine Thiemer, Peter Dörsch, Ulrich Pulg, Sebastian Stranzl, Gaute Velle and Devanshi Pathak

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## Introduksjon

Vassdragsregulering for produksjon av elektrisitet kan fremme masseutvikling av undervannsplanter, slik som krypsiv *Juncus bulbosus* (L.). Plantene blir ofte ansett som et hinder for menneskelige aktiviteter som båttrafikk, bading, og fiske, samt hydrologien i systemet. Uønsket plantevekst fører til kostbare utbedringstiltak med variabel effekt. Spredning av planter kan endre akvatisk biodiversitet og økosystemfunksjon. Vannplantene fjernes ofte mekanisk ved hjelp av klipping. Kunnskap om planteveksthastighet og faktorer som kan påvirke veksten kan være til hjelp når forvaltningen skal ta beslutninger om å fjerne planter fordi det vil gjøre det mulig å få bedre estimater av hvor raskt vannvegetasjonen vokser tilbake igjen etter fjerning.

Elven Otra ligger i Sør-Norge og renner gjennom skoger i fjellandskap. Otra er mye brukt til vannkraftproduksjon. Strekningen studert her drenerer ca. 1900 km<sup>2</sup>, for det meste gjennom Brokke kraftverk, og utslippet er sterkt regulert med karakteristiske døgnvariasjoner (effektkjøring) for å imøtekomme etterspørselen etter elektrisitet. Vannkraftverket slipper periodisk ut vann som er svært overmettet (ca 200 %) av oppløste gasser på grunn av luftinnblanding i vanninntakene. Fisk og virvelløse dyr som puster i gassovermettet vann overmettet kan utvikle gassblæresyke (tilsvarende som dykkersyke hos mennesker), med subakutt dødelighet fra ca. 110 % TDG hos laks (*Salmo salar*).

Masseutvikling av krypsiv i Rysstadbassenget i Otra ca. 3-7 km nedstrøms Brokke kraftverk hindrer bruk av båt og fiske. Drivende plantemateriale kan også tette innløpet Hekni vannkraftverk som ligger nedstrøms Rysstadbassenget. Basert på *in-situ* konsentrasjoner og publiserte laboratorieeksperimenter, kan mengden CO<sub>2</sub> som er løst i vannet være en begrensende faktor for fotosyntesen i Otra. Hvis mengden oppløst CO<sub>2</sub> økes under overmetningshendelser, kan akvatisk fotosyntese øke. Dette kan igjen føre til økt produksjon av O<sub>2</sub> og økt total overmetning av oppløst gassiden oppløst O<sub>2</sub> ikke utveksles med atmosfæren like rask som oppløst CO<sub>2</sub>.

Denne studien brukte nye metoder for å estimere endringene i fotosyntese gjennom døgnet under varierende gassovermetning og gjennom ett års syklus i Rysstadbassenget. Prediktive modeller for plantefotosyntese basert på temperatur og lystilgjengelighet ble brukt for å generalisere funnene og finne effekten av å fjerne ulike mengder krypsiv. Mer spesifikt vil vi svare på tre spørsmål:

1. Kan gassovermetningshendelser fra Brokke kraftverk øke mengden oppløst CO<sub>2</sub> og øke vannplantenes fotosyntese?
2. Kan vannplanters fotosyntese øke gassovermetningen i vannet, og dermed øke risikoen for gassblæresyke hos fisk?
3. Hvor raskt kan krypsiv vokse etter mekanisk fjerning?

## Metoder

Vannprøver ble samlet for for å bestemme mengden av oppløste gasser ( $O_2$ , Argon,  $CO_2$ ) ved inngangen (Rysstad) og nedstrømsenden (Straume) av Rysstadbassenget hver andre time i løpet av 24 timer den 12.-13. og 25.-26. juni 2020. Dette var under perioder med høy gassovermetning (TDG > 140% i utløpet av vannkraftstasjonen). Vi utviklet en ny metode,  $O_2$ :Argon-metoden, for å skille mellom endringer i oppløst  $O_2$  grunnet fysiske prosesser (overmetning av oppløst gass fra vannkraftverk) og biologiske prosesser (fotosyntese og respirasjon). Vi sammenlignet disse resultatene med målinger gjort i august 2019 under en periode med lav TDG-overmetning.

Vi installerte en målestasjon i nedstrømsenden av Rysstadbassenget for å estimere og forutsi endringer i fotosyntesen gjennom året. Stasjonen logget oppløst  $O_2$ , temperatur og lys hvert 15. minutt fra 25. november 2019 til 26. november 2020. En ekstra  $O_2$ -sensor ble utplassert ved innløpet til Rysstadbassenget i samme periode. Vi overvåket også totalt oppløste gasser i utløpet av Brokke kraftverk. Data på vannføring ble levert av vannkraftselskapet (Otra Kraft). Vi estimerte daglig akvatisk fotosyntese med en ny modell basert på en massebalanse av  $O_2$ .

Til slutt kombinerte vi en prediktiv modell for vannplanters fotosyntese med publiserte eksperimentelle data fra Mandalselva for å finne hvordan masseutvikling av planter og fotosyntese kan påvirkes av mekanisk plantefjerning over en fireårsperiode. Vi testet modellen med løpende overvåking i Rysstadbassenget før og etter mekanisk fjerning av krypsiv i juni 2020.

## Resultater og diskusjon

Vi fant at konsentrasjonene av  $CO_2$  ved inngangen (Rysstad) og utløpet (Straume) til Rysstadbassenget var like, uavhengig av gassovermetning (105-180 % total løste gasser) i utløpet av vannkraftverket. Vi observerte ikke en økning i fotosyntesen til krypsiv, sannsynligvis fordi  $CO_2$ -konsentrasjonene var mer kontrollert av økosystemmetabolisme (respirasjon og fotosyntese). Om noe, var fotosyntesen litt høyere i august 2019 under lav gassovermetning (105-110 %) enn i juni 2020 under høy gassovermetning (140-180 %). **Fotosyntese var altså ikke påvirket av  $CO_2$  og gassovermetning og vi konkluderte med at gassovermetning fra Brokke kraftverk ikke vil føre til økt fotosyntesen hos krypsiv.** En fersk studie antydte faktisk at vannplanter kan redusere gassovermetningen ved at gassbobler felles ut på overflaten av plantene.

Demars et al. (2021) konkluderte med at vannplanters fotosyntese i Rysstadbassenget kan øke total overmetning av oppløst gass (TDG) med opptil 5 %. Dette estimatet var utelukkende basert på en forskjell i gassutvekslingshastighet mellom  $CO_2$  og  $O_2$  ved overflaten. Imidlertid fant vi at akvatisk fotosyntese var flere størrelsesordener høyere enn gassutvekslingshastighetene i Rysstadbassenget og ca. 80 % av oksygenet som ble produsert ble kompensert av  $CO_2$ -opptak. **Fotosyntese vil derfor ikke øke TDG med mer enn 1 % ved overflatevannet, og vil i praksis ikke utgjøre noen ytterligere risiko for fiskehelsen.**

Den årlige overvåkingen av oksygenkonsentrasjoner og bruken av en ny modell viste at fotosyntese til krypsiv var påvirket av lysintensitet og temperatur. Fotosyntesen var lavest om vinteren. Fotosyntesen forble lav til slutten av mai på grunn av lav temperatur, og økte deretter kraftig, holdt seg relativt høy fra juli til september, og avtok med temperatur og lys til vinterminimumet. **Krypsiv kunne drive fotosyntese året rundt, også i vintermånedene. Dette vil ikke skje i samme grad i uregulerte elver som har mer dynamikk, blant annet med kaldere temperatur og isdekke.**

Vi estimerte årlig brutto primærproduksjon (GPP) i Rysstadbassenget til  $271 \text{ g C m}^{-2} \text{ år}^{-1}$ . Hvis vi antar at 50 % (område 20-80 %) av GPP brukes av plantene i respirasjon, så er netto primærproduksjon (dvs. karbonet lagret som biomasse)  $135 (54-217) \text{ g C m}^{-2} \text{ år}^{-1}$ . **Den årlige veksten til krypsiv er**

**derfor 2,4 (1,0-3,8) ganger høyere enn gjennomsnittlig nåværende biomasse i Rysstadbassenget (ca  $57 \pm 8 \text{ g C m}^{-2}$ ). Dermed går sannsynligvis store mengder plantemasse tapt gjennom hydraulisk stress og naturlig mekanisk brudd.** Dette samsvarer med personlige observasjoner av drivende krypsiv nærmest når som helst på året.

Vår modell indikerte at fotosyntesen til krypsiv ville gjenopprettes raskt (sannsynligvis innen to år) etter 50-85 % fjerning. Etter 99 % fjerning vil fotosyntesen forbli under 50 % av kapasiteten etter tre år. Pågående overvåking i Rysstadbassenget bekreftet at krypsiv ble gjenopprettet innen to år etter mekanisk fjerning i juni 2020 av  $72 \pm 17 \%$  biomasse eller  $84 \pm 6 \%$  biovolum ( $\pm se$ ).

### **Konklusjon**

Gassovermettet vann med tilhørende økt  $\text{CO}_2$ -tilgjengelighet førte ikke til en økning i fotosyntese og vekst hos krypsiv. Dette var mest sannsynlig på grunn av rask avgassing av  $\text{CO}_2$  før Rysstadbassenget og sannsynligvis fordi  $\text{CO}_2$ -konsentrasjonene var mer kontrollert av økosystemmetabolisme (respirasjon og fotosyntese). Økt gassovermetning som følge av fotosyntese hos krypsiv utgjorde ingen ytterligere risiko for fiskehelse. Gjenveksten av krypsiv kan bremses dersom man fjerner en stor andel av plantene.. Metodene og resultatene utviklet i denne studien kan bidra til å forstå dynamikken mellom gassovermetning, krypsiv og påvirkning på fisk, samt bidra til å effektivisere tiltakene mot krypsiv.

# 1 Introduction

Many rivers are highly fragmented, and their flow is regulated (Nilsson et al. 2005; Grill et al. 2019). The removal of large hydrological peaks, through water transfer and retention in reservoirs, alters geomorphological processes and may promote the mass development of aquatic submerged plants (Gurnell 2014), even in clear oligotrophic rivers, such as the Otra (Rørslett 1988; Rørslett et al. 1989). The mass development of aquatic plants is a worldwide problem and often seen as a nuisance for human activities, such as boat traffic, swimming, fishing and hydrological functioning of the system (Verhofstad and Bakker 2019; Thiemer et al. 2023). Undesirable plant growth leads to costly remedial actions with variable effectiveness (Rørslett and Johansen 1996; Hussner et al. 2017). Proliferation of plants can alter aquatic biodiversity and ecosystem functioning (Schultz and Dibble 2012; Thiemer et al. 2021; Velle et al. 2022; Misteli et al. 2023). Mechanical harvesting is often used to remove aquatic plants and knowledge of plant growth rate and its main drivers could help management decisions because it enables estimates of how fast the aquatic vegetation will regrow after removal (Thiemer et al. 2021).

Daily whole stream metabolism, photosynthesis and respiration, are strongly controlled by flow regime and light availability (Bernhardt et al. 2022), including in regulated rivers (Hall et al. 2015). Primary production may be more constrained by flow regime than temperature through control on the standing biomass (Junker et al. 2021). Specifically, very high flows can “rip off” aquatic plants and therefore limit the development of “nuisance biomass”. Stream temperature is probably the second most important factor controlling primary production (Demars et al. 2016). Although it is hard to disentangle the role of temperature from light in natural rivers (Huryn et al. 2014), regulated rivers often modify the thermal regime of the water independently of light availability allowing the quantification of its role (Hall et al. 2015). These primary drivers may also interact with nutrient availability (Cross et al. 2022), exchange of nutrients between primary producers and decomposers (Demars et al. 2020) and grazing by consumers (Liess et al. 2009).

The role of gas supersaturation on aquatic plant photosynthesis and possible effects on fish health (see e.g. Lennox et al. 2022; Stenberg et al. 2022) was investigated in a preliminary study in which we explained how aquatic plant photosynthesis may contribute to gas supersaturation (Demars et al. 2021). We used a theory of gas exchange and published laboratory experiments linking plant photosynthesis to CO<sub>2</sub> availability to estimate the *potential* effect of CO<sub>2</sub> supersaturation on aquatic plant growth in the Rysstad basin. While doing work for the MadMacs project (<https://www.niva.no/en/projectweb/madmacs>), we were on site at the time of a major gas supersaturation event, repeated the 24-hour diel survey of gasses dissolved in the river water on the 12-13 and 25-26 June 2020, and analysed the samples. We also installed a monitoring station at the downstream end of the Rysstad basin (Straume) for dissolved O<sub>2</sub>, temperature, and light from 25 November 2019 to 26 November 2020. An additional O<sub>2</sub> sensor was deployed at the entrance of the Rysstad basin (Rysstad) for the same period. We also continued the monitoring of total dissolved gases in the outlet of the Brokke hydropower plant and downstream locations.

Here we test how light, temperature and CO<sub>2</sub> may account for the photosynthesis of a perennial submerged plant, *Juncus bulbosus* (L.), throughout an annual cycle in the River Otra, Rysstad basin (Rysstad to Straume). We developed novel methods to estimate photosynthesis of the whole river

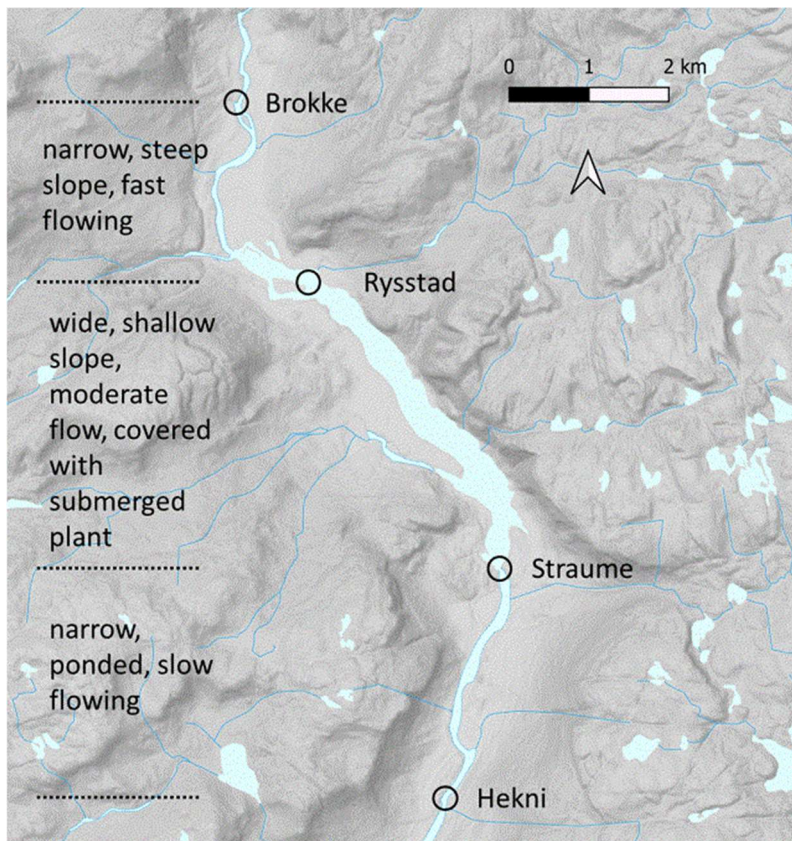
channel with hydropeaking (Pathak and Demars 2023) and supersaturation events (Demars & Dörsch, in preparation). We discuss to what extent plant photosynthesis may increase total dissolved gas saturation, through a differential in gas exchange velocity between CO<sub>2</sub> and O<sub>2</sub> at the water air interface, and whether this poses a risk to fish health.

## 2 Methods

### 2.1 Study area

The River Otra flows through forests and alpine landscapes and is extensively used for hydropower production with water reservoirs and water transfers (Rørslett 1988; Wright et al. 2017). The studied section drains about 1900 km<sup>2</sup>, mostly through Brokke hydropower plant, and discharge is heavily regulated with characteristic diel changes to accommodate demand in electricity (Wright et al. 2017).

The studied river reach Rysstad – Straume shows profuse growth of the perennial aquatic plant *Juncus bulbosus* (L.) 3 to 7.8 km kilometres downstream of the hydropower plant effluent (**Fig. 1**; Rørslett 1988). In June 2020, *J. bulbosus* was harvested mechanically in about 2% of the Rysstad basin (Schneider et al. 2022).



**Figure 1.** Study area with three contrasting river sections.

## 2.2 Data collection

Total dissolved gas (TDG) was recorded every 30 min in the effluent (deep open canal) of the hydropower plant with a Total Gas Analyzer 3.0 (Fisch- und. Wassertechnik; Pulg et al. 2016), based on the Weiss-saturometer principle (Weiss, 1970). The Total Gas Analyzer measures TDG pressure in a submerged gas permeable silicon hose connected to an underwater pressure sensor and an atmospheric pressure sensor above the surface water. The saturation is measured as the percent dissolved air in the water relative to expectation from ambient air pressure. The saturometer has an accuracy of  $\pm 10$  hPa, which is approximately  $\pm 1\%$  TDG. The data were interpolated at 15 min time steps.

A monitoring station placed at Straume (**Fig. 1**) logged at 15-minute intervals dissolved oxygen and water temperature (Xylem-Andeeraa optode 4831), photosynthetic active radiation above the water surface (LICOR, Quantum LI190R-L), air temperature and atmospheric pressure (Barometer RM Young 061302V) using a Campbell datalogger (CR1000X). The oxygen sensor at Straume was inserted in a white plastic pipe fixed to the bridge and protruding in the main current at about 1 m depth. An additional oxygen optode (miniDOT PME, also recording temperature) was fixed on a post mid-column in the main water current at the top of the reach (Rysstad, **Fig. 1**). The oxygen optodes (*in-situ* sensors) were cross calibrated in river water with saturated air using an air bubbler in a small tank by the side of the river, as in previous studies (e.g., Demars 2019).

Hourly discharge data were available from the hydropower company just downstream of the hydropower plant effluent (Brokke) and 11 km downstream at the Hekni dam (**Fig. 1**). Discharge was interpolated at 15 min time steps and a flow routing model was developed to obtain discharge at Rysstad and Straume (Pathak and Demars 2023). Water depth  $z$  was deduced from a bathymetric survey, water level sensors and discharge at Straume. Water velocity (solute mean travel time) was derived from peaks in total dissolved gases or Manning equation. For more details see (Pathak and Demars 2023). The gas exchange coefficient  $k=0.36 \text{ day}^{-1}$  was estimated between Rysstad and Straume using floating flux chambers (Bastviken et al. 2015) and was found to be independent of water temperature and discharge (Pathak and Demars 2023).

We studied three diel cycles in August 2019 (4-5<sup>th</sup>) and June 2020 (12-13<sup>th</sup> and 25-26<sup>th</sup>) with varying gas supersaturation. Water samples were collected by hand at two sites every two hours over 24 hours on both sides of the river, 3 km (Rysstad) and 7.8 km (Straume) downstream of the hydropower plant effluent where the river channel is more constrained. Water bottles were filled to the rim and capped underwater with rubber seals, then crimped. Mercuric chloride ( $\text{HgCl}_2$ ) was immediately added to stop biological processes (100 $\mu\text{L}$  of half saturated solution per 120 mL bottle). We checked that the addition of  $\text{HgCl}_2$  did not affect the determination of  $\text{CO}_2$  (Borges et al. 2019; Koschorreck et al. 2021). The samples were kept cool ( $+4^\circ\text{C}$ ) and in the dark until the day of gas analysis (at the end of the field season) by gas chromatography (Demars and Dörsch, in preparation).

Plant biomass (roots and shoots) was estimated from 0.12 m<sup>2</sup> quadrats laid on patches of *J. bulbosus* before and after mechanical harvesting in control and impacted areas ( $n=20$ , June 2020). Plant patch height and plant cover were estimated from point records along transects in both the control and impacted areas, before and after plant mechanical removal in June 2020 (see Schneider et al. 2022).

The efficiency of harvesting was quantified as average standing biomass (patch biomass x plant cover) or average biovolume (patch height x plant cover, L m<sup>-2</sup>).

### 2.3 The O<sub>2</sub>:Ar method to determine aquatic plant photosynthesis

We used the noble gas argon with similar diffusion and solubility properties to oxygen. We combined the oxygen to argon ratio and *in-situ* oxygen sensor (optode) to estimate stream metabolism (both photosynthesis and respiration). We could then test if supersaturation events could boost the (non-desired) mass development of *Juncus bulbosus* through added supply of CO<sub>2</sub> (Demars et al. 2021).

We calculated the net ecosystem production (photosynthesis – respiration) as follows:

$$NEP_t = \left( \frac{C_t - C_{t-\Delta t}}{\Delta t} - k(C_s - C_t) \right) z \quad (1)$$

with NEP (g O<sub>2</sub> m<sup>-2</sup> hour<sup>-1</sup>),  $\Delta t$  time interval (two hours),  $k$  gas exchange coefficient (hour<sup>-1</sup>),  $C_s$  saturated concentration of oxygen (mg O<sub>2</sub> L<sup>-1</sup> or g O<sub>2</sub> m<sup>-3</sup>),  $C_t$ , concentration of oxygen at time  $t$  (mg O<sub>2</sub> L<sup>-1</sup> or g O<sub>2</sub> m<sup>-3</sup>),  $z$  average stream water depth (m).

This simple model assumed that all changes in oxygen as well as the saturation deficit are due to biological processes. This assumption does not apply where gas supersaturation occurs due to physical processes, such as downstream of a natural cascade, white water or engineering structures (e.g. hydropower plant). Thus the concentrations of oxygen determined by gas chromatography (GC) were corrected to remove small analytical discrepancies between samples using the O<sub>2</sub>:Ar ratio and a correction for analytical errors and natural physical processes leading to gas under- or over-saturation:

$$C = \frac{C_{GC,O_2}}{C_{GC,Ar}} \overline{C_{Ar}} \quad (2)$$

with  $\overline{C_{Ar}}$  in-situ daily average concentration of argon back calculated as in Eveleth et al. (2014) from

$$C_{Ar} = \frac{C_{optode,O_2}}{C_{GC,O_2}} C_{GC,Ar} \quad (3)$$

with  $C_{optode,O_2}$  oxygen concentration from *in-situ* optode.

*Juncus bulbosus* photosynthesis or gross primary production (GPP, g O<sub>2</sub> m<sup>-2</sup> day<sup>-1</sup>) was derived from

$$NEP_t = GPP_t - ER_t \quad (4)$$

with  $ER$  ecosystem respiration (g O<sub>2</sub> m<sup>-2</sup> hour<sup>-1</sup>) estimated during the night hours and assumed constant throughout the day.

Calculations were done in Excel (Microsoft) assuming measurement errors of three key parameters were normally distributed for the propagation of uncertainties using 1000 Monte Carlo simulations (Demars and Dörsch, in preparation).

## 2.4 Annual changes in aquatic plant photosynthesis

Since submerged *J. bulbosus* covered a large part of the sandy river bed (river section Rysstad-Straume, **Fig. 1**), plant photosynthesis may be assessed at the river reach scale using an open channel diel change in oxygen method. We developed a new model integrating and expanding the whole stream metabolism approach (Odum 1956) with a modified flow routing model similar to Sincock and Lees (2002) to estimate plant gross primary production. The observed net ecosystem production (NEP, g O<sub>2</sub> m<sup>-2</sup> min<sup>-1</sup>) at time  $t$  was estimated with an accounting two-station open channel method (Pathak and Demars 2023), as follows:

$$NEP_t = \left( \frac{C_{t+\Delta t} - C_t}{\Delta t} - \frac{Q_{i,t-\alpha}}{Q_t \times T_{sadv}} (C_{i,t-\alpha} - C_t) - k(C_{s,t} - C_t) \right) z_t \quad (5)$$

and

$$\alpha = F_{adv} \times T_{sadv} \quad (6)$$

$C_t$ , oxygen concentration at time  $t$  (mg O<sub>2</sub> L<sup>-1</sup> or g O<sub>2</sub> m<sup>-3</sup>),  $\Delta t$  time interval (15 min),  $C_s$  saturated oxygen concentration (mg O<sub>2</sub> L<sup>-1</sup> or g O<sub>2</sub> m<sup>-3</sup>),  $Q_{i,t-\alpha}$  incoming discharge at the top of the reach (m<sup>3</sup> min<sup>-1</sup>) at time  $t - \alpha$ ,  $\alpha$  advection delay (min),  $F_{adv}$  advection coefficient (unitless),  $T_{sadv}$  mean solute travel time (min),  $Q_t$  outgoing discharge at the bottom of the river reach (same unit as  $Q_i$ ),  $k$  gas exchange rate (min<sup>-1</sup>),  $C_{i,t-\alpha}$  incoming oxygen concentration (mg O<sub>2</sub> L<sup>-1</sup> or g O<sub>2</sub> m<sup>-3</sup>) at time  $t - \alpha$ ,  $C_t$  outgoing oxygen concentration at time  $t$ , and  $z_t$  average stream water depth (m).

Gross primary production (GPP, g O<sub>2</sub> m<sup>-2</sup> min<sup>-1</sup>) was derived from:

$$NEP_t = GPP_t - ER_t \quad (7)$$

with  $ER$  ecosystem respiration (g O<sub>2</sub> m<sup>-2</sup> min<sup>-1</sup>) estimated during the night hours and assumed constant throughout the day.

Note here  $ER$  is not reported in this study as it was too often biased by total dissolved gas supersaturation from the hydropower plant (see Hall et al. 2015). The model was parameterised as in Pathak and Demars (2023). Calculations were done in Excel (Microsoft) assuming measurement errors of four key parameters were normally distributed for the propagation of uncertainties using 1000 Monte Carlo simulations. We only retained results when TDG average in the effluent of the hydropower plant was within 90-130%, the TDG standard deviation during the day was within 10% and when the maximum within a day did not exceed 140% (to avoid periods when the water was fizzing within the studied reach).

Note also that the gas exchange rate was low relative to biological processes (photosynthesis and respiration), suggesting that the term  $-k(C_{s,t} - C_t)$  in **Eq. 5** could have been neglected in this case study. One practical implication here is that the differential in O<sub>2</sub> and CO<sub>2</sub> gas exchange at the water-air interface will not lead to TDG supersaturation as previously hypothesised (Demars et al. 2021).



## 2.5 Prediction of aquatic plant growth

The thermodynamic theory of enzyme kinetics can be simplified to an Arrhenius model of temperature dependence within the physiological temperature range (4-45°C in Demars et al. 2016). We centred the temperature response function at  $T_C = 283 K = 10^\circ C$  similarly to Gillooly et al. (2001):

$$GPP_T = GPP_{T_C} \exp \left[ E_a \left( \frac{1}{kT_C} - \frac{1}{kT} \right) \right] \quad (8)$$

with  $GPP_T$  and  $GPP_{T_C}$  being gross primary production ( $g O_2 m^{-2} day^{-1}$ ) at temperature  $T$  and centred temperature  $T_C$ , respectively,  $E_a$  activation energy of autotrophs (0.57 eV), and  $k$  Boltzmann constant ( $8.62 \cdot 10^{-5} eV K^{-1}$ ). In order to model light independently of temperature, the same equation (but inverting  $T$  and  $T_C$ ) was first used to standardise the observed  $GPP_T$  to GPP at  $10^\circ C$  ( $GPP_{T_C}$ ) and then regress  $GPP_{T_C}$  against light using a Michaelis-Menten equation:

$$GPP_{T_C} = \frac{GPPmax_{T_C} PAR}{k_{PAR} + PAR} \quad (9)$$

with  $GPPmax_{T_C}$  being the maximum GPP at  $10^\circ C$ , and  $PAR$  photosynthetic active radiation ( $mol quanta m^{-2} day^{-1}$ ), and  $k_{PAR}$  the  $PAR$  at which half the  $GPPmax_{T_C}$  is realised.  $GPPmax_{T_C}$  and  $k_{PAR}$  were fitted parameters using a non-linear regression model in R (R Core Team 2020).

Thus, the full predictive model with independent light and temperature effect was:

$$GPP_T = \frac{GPPmax_{T_C} PAR}{k_{PAR} + PAR} \exp \left[ E_a \left( \frac{1}{kT_C} - \frac{1}{kT} \right) \right] \quad (10)$$

Observed GPP was then regressed against the predictive model to determine the proportion of variance explained by the model.

## 2.6 Prediction of aquatic plant photosynthesis following mechanical harvesting

The above theory can make predictions for warming when the system is near equilibrium (or peak plant mass). In many cases the system will be far from equilibrium, as in the case of introduction of an invasive species, mechanical harvesting or annual plants. Plant colonisation rate may be modelled with a logistic growth curve as follows:

$$\frac{dB}{dt} = \frac{rB(B_{eq} - B)}{B_{eq}} \quad (11)$$

where  $B$  is plant biomass ( $g C m^{-2}$ ) at time  $t$ ,  $B_{eq}$  is plant biomass ( $g C m^{-2}$ ) at equilibrium, and  $r$  plant expansion rate ( $day^{-1}$ ).

The above equation can be generalised to modelling the proportion of biomass relative to equilibrium with  $x = B/B_{eq}$  and we now have:

$$\frac{dx}{dt} = rx(1 - x) \quad (12)$$

with solution:

$$x_t = \frac{1}{1 + \left(\frac{1}{x_0} - 1\right) e^{-rt}} \quad (13)$$

If we assume plant photosynthesis to be linearly dependent on biomass then we have:

$$GPP_{T,t} = x_t \frac{GPPmax_{TC} PAR}{k_{PAR} + PAR} \exp \left[ E_a \left( \frac{1}{kT_C} - \frac{1}{kT} \right) \right] \quad (14)$$

Now we can study how GPP changes with varying  $x_0$  representing, e.g., the efficiency of mechanical harvesting (% removal of biomass) and varying  $r$  representing, e.g., how fast an invasive species recolonises following harvesting. Here we inferred  $r$  from removal experiments in the regulated River Mandalselva (Johansen 2002), flowing parallel to the River Otra with similar environmental characteristics (Moe and Demars 2017).

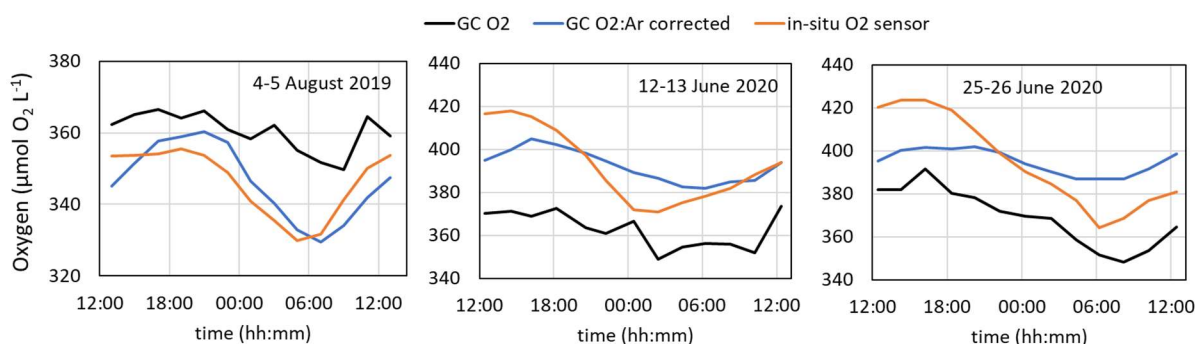
Johansen (2002) reported three experiments: 72% plant removal by machine and 99% plant removal by hand in 50 m<sup>2</sup> and 100 m<sup>2</sup> plots, all done in 1996. The mechanical plant removal time series was re-aligned to have corresponding plant cover (28% cover in 1996 for mechanical removal and average 27% plant cover in 1998 for removal by hand). These data allowed to infer the expansion rate per year, which we converted to per day, and implicitly assumed to be valid at our centred temperature  $T_C = 10^\circ C$ .

In order to better visualise the results, we used *potential* daylight availability and a sine function for temperature while keeping the observed range and time lag in light and temperature of our study site. We set  $x_0 = 0.01$  (corresponding to the 1% cover or 99% removal in the hand removal experiments) to infer the parameter  $r$  from a non-linear regression model in R (R Core Team 2020).

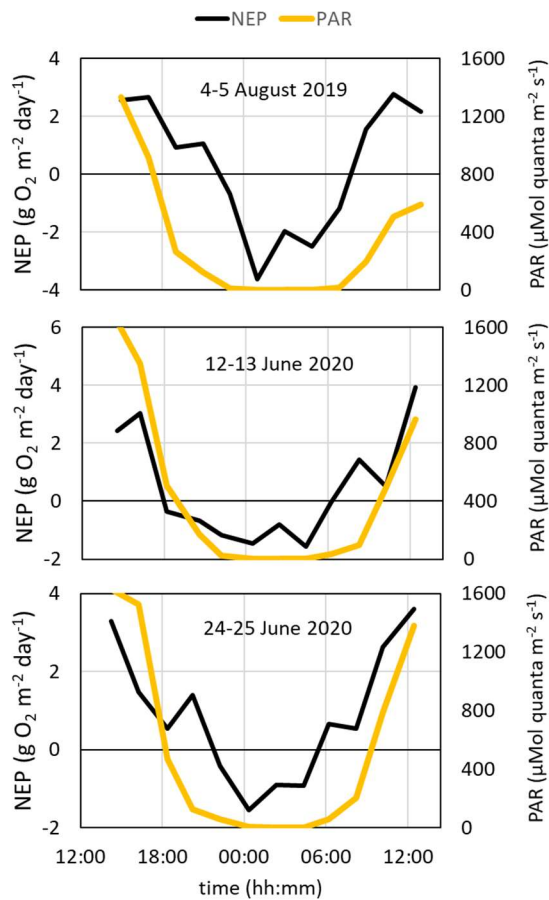
## 3 Results and discussion

### 3.1 Role of CO<sub>2</sub>

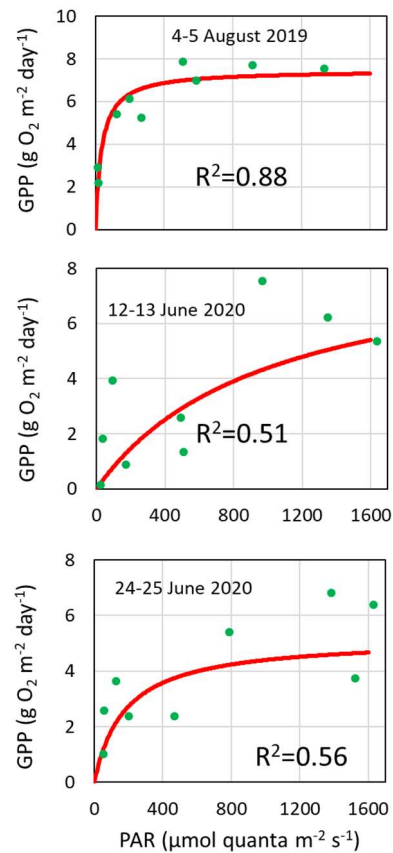
The oxygen concentrations determined by gas chromatography were somewhat off the oxygen concentrations produced by the *in-situ* optode: over estimation in August 2019 and under estimation in June 2020 (Fig. 2). The applied corrections aligned the GC oxygen concentrations with the *in-situ* O<sub>2</sub> concentrations. In August 2019, the amplitude remained similar as there was little evidence of physical supersaturation from the effluent of the hydropower plant (105-110% total dissolved gas saturation, Demars et al. 2021). In June 2020, the diel amplitude of the corrected oxygen concentrations was much shallower than the oxygen sensor (optode) due to very high physical supersaturation of total dissolved gases in the effluent of the hydropower plant: 170% on the 12-13<sup>th</sup> June and 145% on the 25-26<sup>th</sup> June. Under such high supersaturation events the water fizzes downstream of the effluent leading to large losses in total dissolved gas supersaturation within the first three kilometres (Pulg et al. 2016; Pulg et al. 2022). We did not observe a boost in aquatic plant photosynthesis, likely because the CO<sub>2</sub> concentrations were more controlled by ecosystem metabolism (respiration and photosynthesis) – Demars and Dörsch (in preparation). Average ( $\pm$ sd) concentrations of CO<sub>2</sub> three kilometres downstream of the effluent at Rysstad (54 $\pm$ 20, 27 $\pm$ 3, 30 $\pm$ 4  $\mu$ Mol CO<sub>2</sub> L<sup>-1</sup>) were similar to that at Straume (44 $\pm$ 9, 30 $\pm$ 7, 33 $\pm$ 7  $\mu$ Mol CO<sub>2</sub> L<sup>-1</sup>) on the three sampling dates, independent of total dissolved gas saturation. The standardisation of the oxygen curves through the O<sub>2</sub>:Ar ratio provided nice sinusoidal curves as expected from the low gas exchange rate (<1 day<sup>-1</sup>) and high biological activity (Fig. 2, Demars et al. 2015).



**Figure 2.** Oxygen concentrations determined by gas chromatography (GC) without and with the O<sub>2</sub>:Ar correction at Straume, and comparison with *in-situ* oxygen sensor.



**Figure 3.** Diel changes in net ecosystem production (NEP) and photosynthetic active radiation (PAR).



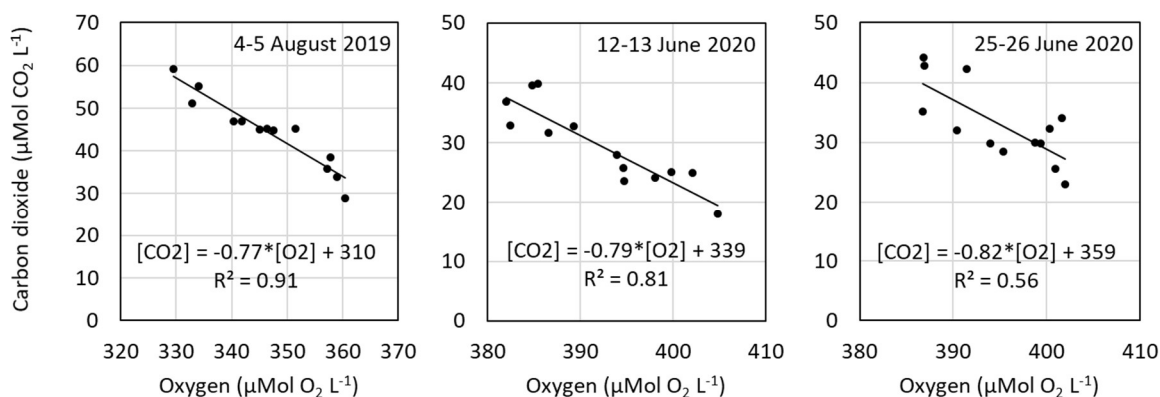
**Figure 4.** Gross primary production as a function of light (photosynthetic active radiations), dots are observed data and curves are Michaelis-Menten type model.

The net ecosystem production (NEP) is the metabolic balance between photosynthesis and respiration. It is negative when respiration exceed photosynthesis. NEP changed according to light (**Fig. 3**) becoming negative at night when respiration processes exceeded photosynthesis. Assuming respiration was constant at night, we demonstrate that GPP was highly related to light availability (photosynthetic active radiation, **Fig. 4**). We also found a strong relationship between  $O_2$  and  $CO_2$  concentrations with a negative slope approaching 1:1, as expected from the photosynthesis chemical reaction where one molecule (or mole) of  $O_2$  is produced from one molecule (or mole) of  $CO_2$  uptake (**Fig. 5**). The lower than 1:1 slope (about -0.8) may be explained by the flux of  $CO_2$  between the water and the atmosphere being 13 times faster for  $CO_2$  than  $O_2$ , even in the absence of bubble mediated gas transfer or bicarbonate formation (Demars et al. 2021). The slopes were consistent independently of the degree of total dissolved gas supersaturation in the effluent, suggesting the hydropower plant did not significantly affect  $CO_2$  supersaturation at the study site (Rysstad basin), as described above.

The metabolic estimates, summarised in **Table 1**, were slightly higher in August 2019 than in June 2020, even after correcting for temperature (see **section 3.3**). Overall, our estimates of summer daily photosynthesis exceeded respiration, which was expected at this time of year (short night, high light) in a sandy riverbed with a relatively high standing biomass of submerged *Juncus bulbosus* throughout the water column.

Carbon dioxide concentrations in the water column were halved at the peak of photosynthesis (**Fig. 5**) and CO<sub>2</sub> concentrations (20-60 μMol CO<sub>2</sub> L<sup>-1</sup>) were well below the level necessary to saturate underwater photosynthesis of the leaf apparatus of *Juncus bulbosus* (over 500 μMol CO<sub>2</sub> L<sup>-1</sup>, Roelofs et al. 1984; Sand-Jensen 1987). An increase in *Juncus bulbosus* growth rate was observed when CO<sub>2</sub> was added (×10) to the water column in a lake with highly organic sediment and background CO<sub>2</sub> concentration around 50 μMol CO<sub>2</sub> L<sup>-1</sup> (Svedang 1992). Efficient internal gas recycling and CO<sub>2</sub> root uptake could, however, partly alleviate CO<sub>2</sub> limitation (Wetzel et al. 1984; Wetzel et al. 1985) with sediment pore water concentrations averaging 170 μMol CO<sub>2</sub> L<sup>-1</sup> (Moe and Demars 2017). So other nutrients may be more limiting *Juncus bulbosus* plant growth, as inferred from plant stoichiometry (Moe et al. 2021). The hypothesised role of the hydropower plant boosting plant photosynthesis (Demars et al. 2021) can be dismissed as we found no evidence of higher CO<sub>2</sub> concentrations at the top of the reach (Rysstad) with mass development of *Juncus bulbosus* compared to the bottom of the reach (Straume), even during the total gas saturation events (**Fig. 5**).

A recent study also suggested that aquatic plants may in fact reduce TDG in the water column by increasing the rate of bubble formation and gas evasion rate to the atmosphere (Yuan et al. 2018).



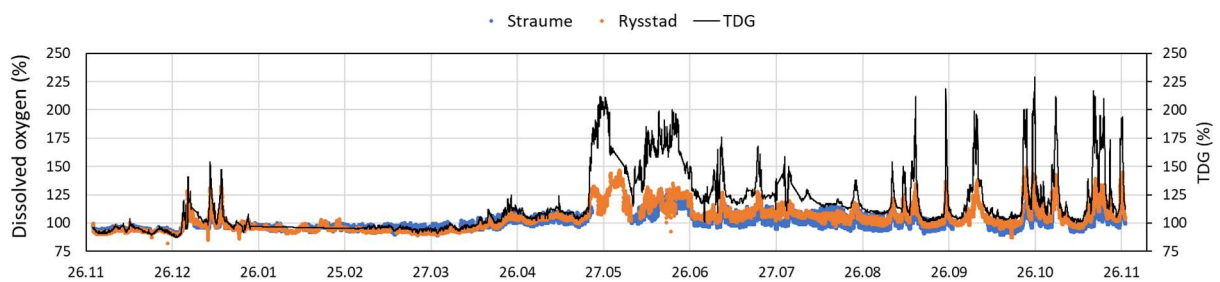
**Figure 5.** Tight relationships between carbon dioxide and oxygen concentrations.

**Table 1.** River Otra conditions (range) and metabolic estimates from Monte Carlo simulations (median and 95% confidence interval). \* just outside the hydropower plant effluent at Brokke, TDG total dissolved gasses, ER ecosystem respiration, GPP gross primary production.

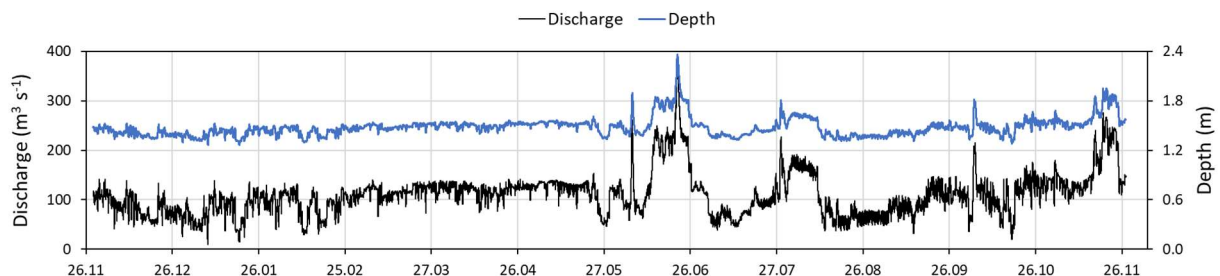
Dates	TDG*	Discharge	Velocity	Depth	ER	GPP
	%	m <sup>3</sup> s <sup>-1</sup>	m s <sup>-1</sup>	m	g O <sub>2</sub> m <sup>2</sup> day <sup>-1</sup>	g O <sub>2</sub> m <sup>2</sup> day <sup>-1</sup>
4-5 August 2019	105-110	28-72	0.09-0.19	1.29-1.38	-3.9 (-3.0 to -4.7)	5.7 (4.5-7.0)
12-13 June 2020	160-180	129-201	0.30-0.49	1.50-1.75	-2.4 (-1.9 to -2.9)	2.9 (2.4-3.4)
25-26 June 2020	140-150	159-228	0.39-0.53	1.60-1.81	-1.6 (-1.2 to -2.1)	3.8 (3.2-4.5)

### 3.2 Annual cycle of aquatic plant growth

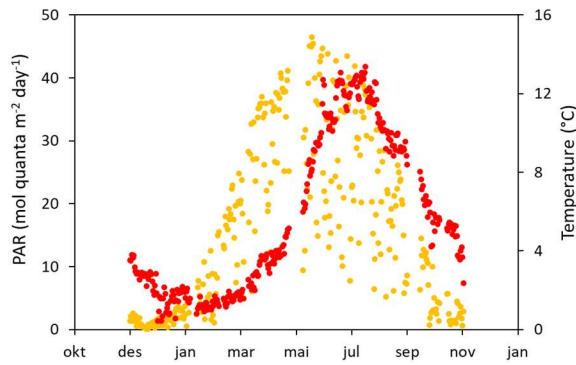
Large peaks of total dissolved gases (TDG), up to over 200% in the hydropower plant effluent, were observed throughout the year (Fig. 6), somewhat independently of river discharge (Fig. 7), as previously observed (Pulg et al. 2016). Those TDG supersaturation events were mirrored by the oxygen concentrations (Fig. 6). There were also periods throughout the year with no TDG supersaturation and more stable TDG. River water temperature was largely unrelated to light availability (Fig. 8), as expected, since hydropower regulation alters natural water temperature in high head systems in northern rivers (Heggenes et al. 2021), including the river Otra (Moe and Demars 2017). The average GPP (straight calculations) was highly related to the median GPP with small uncertainties determined by random Monte Carlo simulations (Fig. 9).



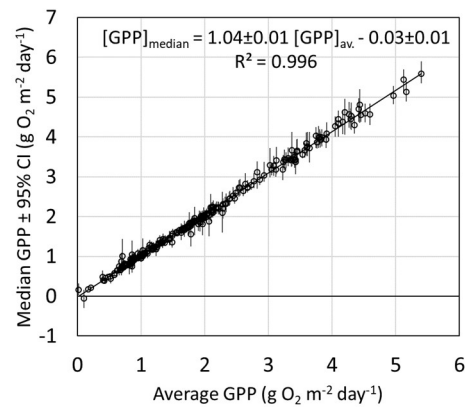
**Figure 6.** Dissolved oxygen saturation (%) at Rysstad (top of the reach) and Straume (bottom of the reach); and total dissolved gases saturation (TDG, %) during the annual cycle (Dec 2019-Nov 2020).



**Figure 7.** Measured discharge at Hovet (3.5 km upstream the studied reach) and associated changes in river water depth within the studied reach Rysstad-Straume during the annual cycle (Dec 2019-Nov 2020).



**Figure 8.** River Otra decoupling of light availability (yellow) and temperature (red) during an annual cycle (December 2019–November 2020).



**Figure 9.** Average gross primary production (GPP) highly related to GPP determined by Monte Carlo simulations.

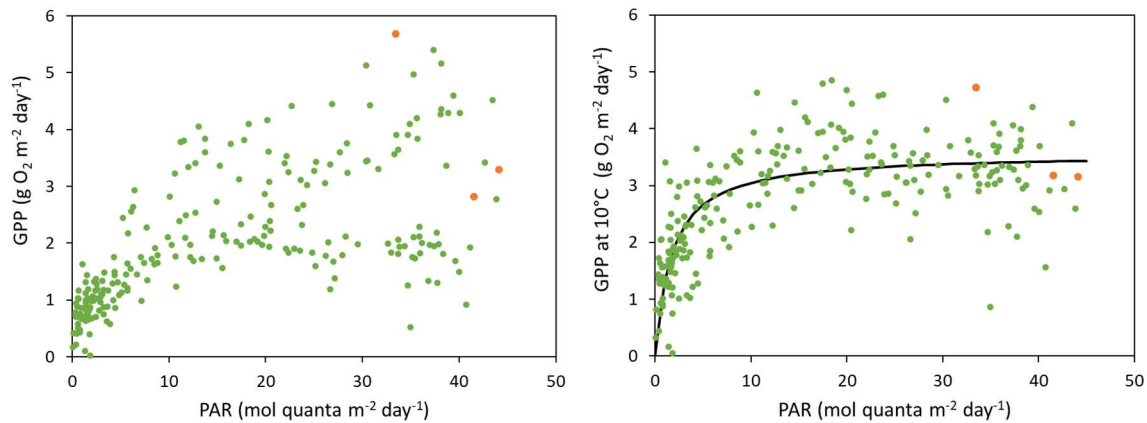
### 3.3 Prediction of aquatic plant growth

Gross primary production was much better related to light after taking into account the effect of temperature with  $GPP_{max_{TC}} = 3.62 \pm 0.07 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$  and  $k_{PAR} = 1.67 \pm 0.18 \text{ mol quanta m}^{-2} \text{ day}^{-1}$  (**Fig. 10**). The full light-temperature model explained 87% of the variance in observed GPP (**Fig. 11**). The model also fitted GPP observed during large supersaturation events (with TDG 140–180%) using an  $\text{O}_2:\text{Ar}$  ratio method (**Fig. 11**, Demars and Dörsch, in preparation).

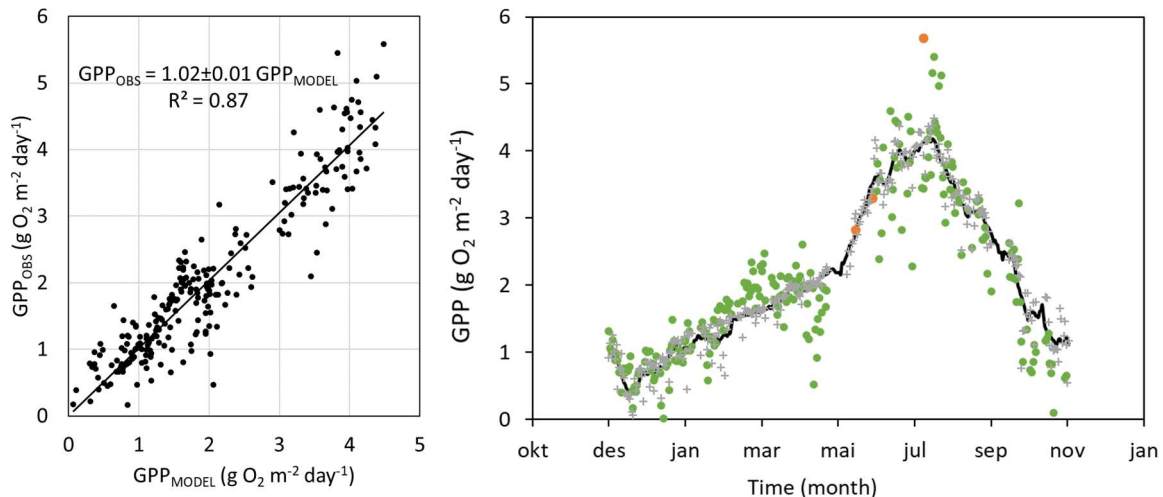
The sum of GPP throughout the year was  $271 \text{ g C m}^{-2} \text{ year}^{-1}$ , assuming a respiratory quotient of one. If we assume that 50% (range 20–80%) of GPP is lost through autotrophic respiration (Demars et al. 2015; Demars et al. 2017), then net primary production is 135 (54–217)  $\text{g C m}^{-2} \text{ year}^{-1}$ . The annual growth is therefore 2.4 (1.0–3.8) times the average ( $\pm$ se) standing biomass of *Juncus bulbosus* over the reach ( $57 \pm 8 \text{ g C m}^{-2}$ ). This suggests some continuous plant mass loss through hydraulic stress and natural mechanical break of stems.

Our results suggest that a simple model with just two independent drivers (PAR and temperature) was sufficient to model GPP in the river Otra. This is likely because neither the standing biomass of *Juncus bulbosus* nor key nutrients ( $\text{CO}_2$ , dissolved inorganic N, soluble reactive P) changed much throughout the year (Moe and Demars 2017): the Otra ecosystem was at near steady-state.

Since we measured PAR above the water surface, light availability could be varying with water depth and turbidity (Hall et al. 2015). The water of the river Otra remains very clear throughout the year, except during the hydrological peak due to snowmelt in June. We checked that water depth was not related to the residual of the model. The standing biomass of *Juncus bulbosus* is also resilient to hydropeaking in the river Otra, in contrast to the green algae of the Colorado river (Hall et al. 2015). In the river Otra, continuous loss of biomass was likely to occur innocuously to balance continuous growth.



**Figure 10.** Daily gross primary production (GPP) as a function of light (photosynthetic active radiations, PAR) without (left) and with (right) a temperature correction. The curve is a Michaelis-Menten type model fitted to daily GPP at 10°C. The three datapoints in orange were determined with the O<sub>2</sub>:Ar method.



**Figure 11.** Observed gross primary production (GPP<sub>OBS</sub>) can be accurately predicted using just two independent factors: light (photosynthetic active radiations, PAR) and temperature (left graph). The model (grey cross with moving average black line) could depict the daily GPP changes (green dot) remarkably well throughout the year (right graph). The three datapoints in orange were determined with the O<sub>2</sub>:Ar method.

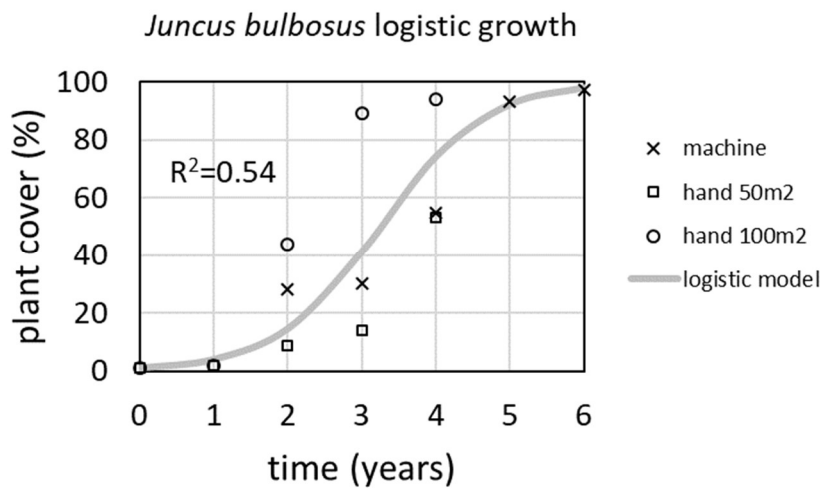
### 3.4 Prediction of aquatic plant photosynthesis following mechanical harvesting

From the three published *J. bulbosus* removal experiments and observed re-growth (1996-2000), we were able to infer an expansion rate ( $\pm$ se)  $r = 1.41 \pm 0.10 \text{ year}^{-1}$  with  $x_0 = 0.01$  ( $R^2=0.54$ , **Fig. 12**). We used  $r = 1.41$  for our plant removal simulations (**Fig. 13**). The simulations suggest that *J. bulbosus* would regrow rapidly following 50-85% removal, while near total removal would keep photosynthesis below 50% of its equilibrium capacity for three years (**Fig. 13**).

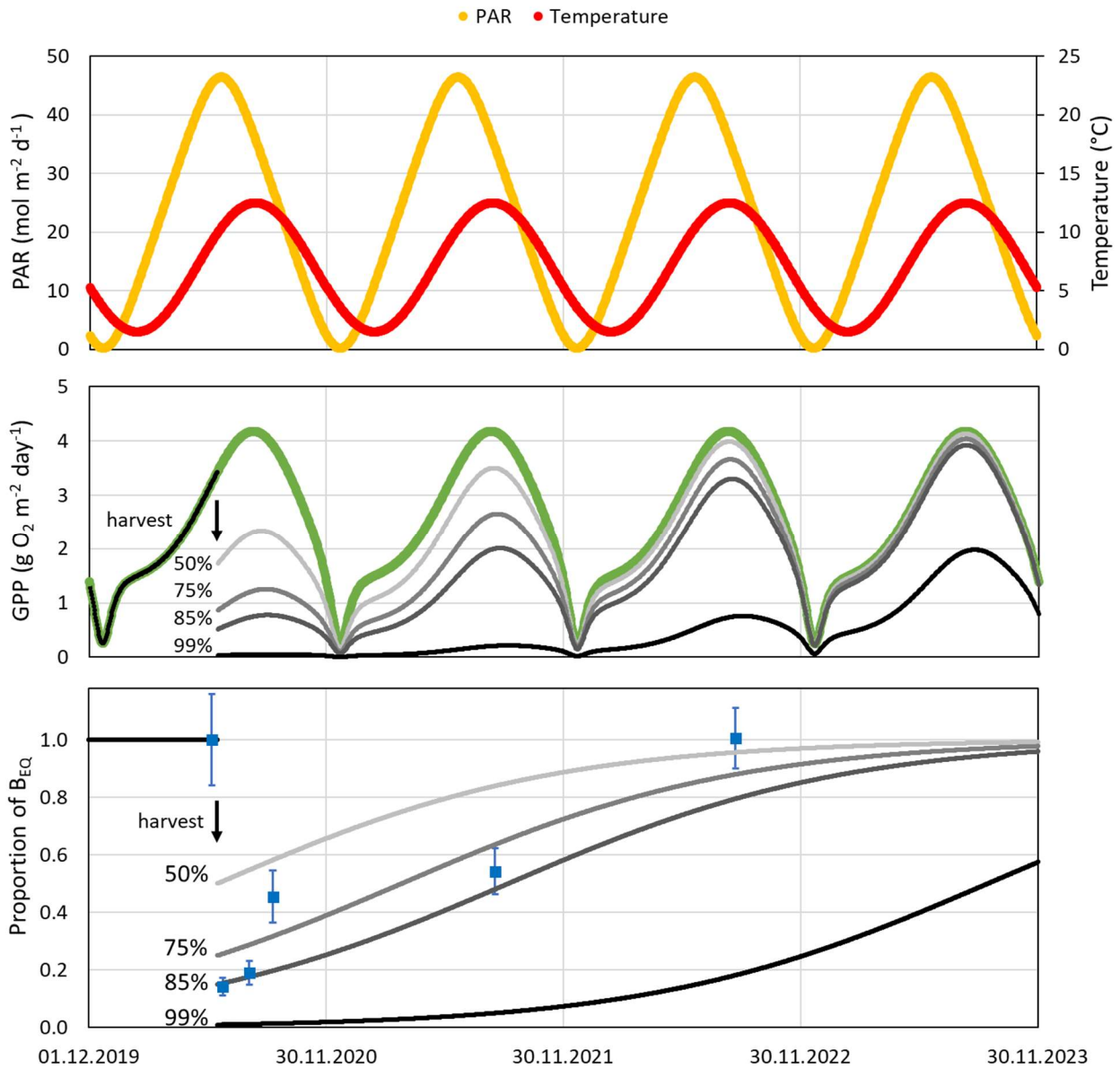


Significant removal of plant biomass (30% cover removed) was only achieved through lowering the water level in mid-winter ( $-10^{\circ}\text{C}$ ) for five days to freeze the river bed, followed by increasing discharge from 2 to  $150\text{ m}^3\text{ s}^{-1}$  within an hour (Rørslett and Johansen 1996). However, the root system of *J. bulbosus* remained, the plant regrew rapidly, and the cost was prohibitive to the hydropower company (Rørslett and Johansen 1996). Thus, mechanical harvesting along one side of the river has been the preferred option to manage the outgrowth.

The plant removal scenarios suggested that photosynthetic capacity of *J. bulbosus* at equilibrium was recovered within two years of mechanical harvesting in the range 50-85% removal, and that only near total removal (99%) was able to keep photosynthesis below 50% of its capacity for three years. The model provided general system behaviour, and on-going monitoring in the Rysstad basin confirmed that *J. bulbosus* recovered within two years following plant mechanical removal in June 2020 of  $72\pm 17\%$  biomass or  $84\pm 6\%$  biovolume ( $\pm\text{se}$ ) (Schneider et al. 2022; **Fig. 13**).



**Figure 12.** Changes in plant cover following mechanical harvesting to infer plant expansion rate ( $r$ ).



**Figure 13.** Changes in photosynthetic active radiation (PAR, red line), temperature (yellow line), gross primary production (GPP, green line) and proportion of biomass at equilibrium  $B_{eq}$  (black lines) derived from light-temperature model with scenarios of plant harvest (50-99%). Blue squares with standard errors illustrate observed proportional changes in plant biovolume in area affected by mechanical removal in June 2020 (2% of the area of Rysstad basin).

## 4 Conclusion

*Can supersaturation events from Brokke hydropower plant increase dissolved CO<sub>2</sub> and boost aquatic plant photosynthesis?*

The growth of *Juncus bulbosus* colonising the river channel was revealed under varying supersaturation events using the new O<sub>2</sub>:Ar method. We did not observe a boost in aquatic plant photosynthesis, likely because the CO<sub>2</sub> concentrations were more controlled by ecosystem metabolism (respiration and photosynthesis). In fact, a recent study suggested that aquatic plants may reduce TDG in the water column by increasing the rate of bubble formation and gas evasion rate to the atmosphere.

*Can aquatic plant photosynthesis increase total dissolved gas supersaturation, thereby possibly increasing risk of supersaturation for fish health?*

Demars et al. 2021 concluded that aquatic plant photosynthesis in the Rysstad basin may raise total dissolved gas (TDG) supersaturation by up to 5%. This estimate was entirely based on a differential in gas exchange velocity between CO<sub>2</sub> and O<sub>2</sub> at the water-air interface. However, aquatic photosynthesis was orders of magnitude larger than gas exchange rates in the Rysstad basin and about 80% of the oxygen produced was compensated by CO<sub>2</sub> uptake (**Fig. 5**). Thus, photosynthesis did not increase TDG by more than 1% at the surface water. TDG supersaturation attenuates with about 10% per m water depth due to hydrostatic pressure (Pleizier et al. 2020). Trout in Rysstad occur deep enough (>2 m) to compensate for TDG supersaturation most of the time (Lennox et al. 2022). An increase by 1% TDG at the water surface will constitute virtually no increase at 2 m depth. Thus, photosynthesis poses little additional risk to fish health.

*How fast may Juncus bulbosus grow following mechanical harvesting?*

*Juncus bulbosus* is a perennial plant and was able to grow year-round, with maximum growth rate occurring when both light and temperature were high. The annual net primary production was estimated as 135 (54-217) g C m<sup>-2</sup> year<sup>-1</sup>. The annual growth is therefore 2.4 (1.0-3.8) times the average standing biomass of *Juncus bulbosus* over the reach (57±8 g C m<sup>-2</sup>). This suggests some continuous plant mass loss throughout the year, through hydraulic stress and natural mechanical breakage of stems.

Regrowth following mechanical harvesting was predicted to be rapid (within two years) following a 72±17% reduction in plant biomass or 84±6% reduction in biovolume, and this was confirmed with on-going monitoring in the Rysstad basin (**Fig. 13**).

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