Are flood-driven turbidity currents hot-spots for priming effect in lakes?

D. Bouffard[1] and M-E. Perga[2,*]

[1]{Physics of Aquatic Systems Laboratory, Margaretha Kamprad Chair, EPFL-ENAC-IEE-APHYS, CH-1015 Lausanne, Switzerland}

[2]{INRA-Université Savoie Mont Blanc, UMR 042 CARRTEL, Thonon les Bains, France}

Correspondence to: M-E. Perga (marie-elodie.perga@thonon.inra.fr)

Abstract

In deep stratified lakes, such as Lake Geneva, flood-driven turbidity currents are thought to contribute to the replenishment of deep oxygen by significant transport of river waters saturated with oxygen into the hypolimnion. The overarching aim of this study was to test directly this long-standing hypothesis. It combines direct observational data collected during an extreme flooding event that occurred in May 2015 with dark bioassays designed to evaluate the consequences of riverborne inputs on the hypolimnetic respiration. The exceptional precipitations of May 2015 caused floods with annual return time for the Rhône River, the dominant tributary of Lake Geneva, and with 50-year return time for the Dranse River, the second most important tributary. Sediment loaded river flows generated turbidity currents plunging into the lake hypolimnion. The observed river intrusions contributed to the redistribution of dissolved oxygen, with no net gain, when occurring in the lowermost hypolimnetic layer. In the uppermost hypolimnion above the last deep mixing event, the intrusions coincided with a net oxygen deficit. Consistent with field observations, dark bioassays showed that 1% to 50% substitution of riverine organic matter to deep (<200 m) hypolimnetic water did not affect microbial respiration, while addition of 1 to 10% of riverine water to the uppermost hypolimnetic waters resulted in a respiration overyielding, i.e. excess respiration of both riverborne and lacustrine organic matter. The results of our study conflict the hypothesis that flood-driven turbidity currents necessarily increase hypolimnetic oxygen

stocks in Lake Geneva. In contrast, they show that flood-driven turbidity currents can be potential hot-spots for priming effect in lakes.

1 Introduction

In thermally stratified lakes, river water inflow occurs under two different modes. Under normal (i.e dry-weather) flow conditions, the river water is injected at the interface between the warm, upper layer (epilimnion) and the cold lower layer (hypolimnion), forming an interflow in the upper thermocline (Fischer, 1979) or at the surface. Particularly during flood events, high concentrations of suspended sediments in rivers increase the density of inflowing waters and therefore generate turbid density currents following the slope and flowing into the hypolimnion (i.e. hyperpycnal plume). Their dynamics are divided into three distinct stages (Alavian et al., 1992; Cortés et al., 2014; Hogg et al., 2013). First, the river dense water pushes the ambient lake water, until the resulting baroclinic pressure created by the local density difference between the river and the lake water balance the force of the momentum inflow. At this stage, the river flow plunges (plunging stage), then the flow continues to run along the lake bed as an underflow (underflow regime). The flow eventually reaches the depth of neutral buoyancy, separates from the lake bottom and intrudes into the lake (intrusion stage).

Lake observations of such riverborne turbidity currents date back to the late XIXth century by Forel in Lake Geneva (Forel, 1892), and more recent reports indicate that they occur in many perialpine lakes such as Walensee (Lambert et al., 1976), Lake Geneva (Lambert and Giovanoli, 1988), Lake Lucerne (Wüest et al., 1988), Lake Brienz (Finger et al., 2006), and Lake Lugano (De Cesare et al., 2006). Marine underflows are also common features (Mulder et al., 2003).

Besides their implications on the physical structure of subaquatic environments (Meiburg and Kneller, 2010), underflows have been considered for their potential biogeochemical consequences on lakes. For instance, in Lake Geneva, the long-standing hypothesis has been that river intrusions could replenish deep oxygen, and this hypothesis was supported by several, albeit indirect, field observations. Fahrni and Rapin (1986) compiled the densities of Lake Geneva hypolimnetic waters and those of the Rhône River over seven years and suggested that some of the time-periods prone to river underflows coincided with partial oxygen replenishment in the deepest layers of the lake central area (long-term monitoring station SHL2). Meybeck et al. (1991) pointed out relatively frequent and important oxygen

and silicate anomalies occurring close to the sediment-water interface at the reference monitoring station SHL2 and invoked riverborne underflows, along with alternative mechanisms (accumulation of turbid, cold water on lake banks after severe storms), as being responsible for these anomalies.

Lake Geneva has been suffering from deep water hypoxia since its early eutrophication in the late 1950s (Jenny et al., 2014). Based on the hypothesis of oxygen-rich river water intrusions (Meybeck et al., 1991), underflows following episodes of heavy rainfalls are expected to counteract hypoxia by supplying oxygen to the stratified lake hypolimnion (Jenny et al, 2014). Yet, numerous hydroelectric dams have been constructed on the course of the Rhône River, leading to a shift in the seasonal discharge pattern (Loizeau and Dominik, 2000). Consequently, large floods, mostly occurring in summer, were reduced in amplitude and frequency, also leading to a decrease in sediment input by at least a factor 2 (Loizeau and Dominik, 2000). This summer discharge and bulk plume density reduction impacted the occurrence of underflows along the lake bottom and is thought to aggravate deep water hypoxia. However, despite their crucial functional implications on hypolimnetic oxygen concentrations, the consequences of turbidity currents, and of their further decrease in occurrence, have actually never been investigated directly.

Condition for the riverborne currents to reach the bottom of the central basin is that the hyperpycnal plume does not get diluted by lake water as it advances within a lake (Turner, 1986). Yet, sediment loaded underflows, as those expected during floods, differ from underflows observed during regular river regime, whose density is only controlled by temperature. While the latter typically intrudes in the metalimnion as recently revealed by isotope-tracing (Halder et al., 2013), the former undergoes a dynamic density change, generating multiple underflows and therefore increasing the overall dilution (Cortés et al., 2014). In addition, underflows might primarily act on the hypolimnion by pushing deep waters upwards (Wüest et al., 1988), therefore redistributing oxygen within deep layers, rather than contributing to a net oxygen gain, as observed in nearby Lake Lugano (De Cesare et al., 2006).

Besides these positive and null hypotheses, an alternative, metabolic hypothesis is formulated here based on the observed impact of floods on the carbon budgets of some lakes around the world. A common opinion is that the bulk of the organic carbon that enters surface water is refractory and may poorly contribute to bacterial metabolism, in comparison to autochthonous

sources (Moran and Hodson, 1990). However, the composition and hence quality of dissolved organic matter entering lakes depend on the watershed coverage, land-use, climate and hydrology (Alvarez-Cobelas et al., 2010) and might also be highly variable during the year (Berggren et al., 2009). Increased inputs of fresh organic material during stormwaters and spring floods (Agren et al., 2008; Dhillon and Inamdar, 2013; Raymond and Saiers, 2010) have been shown to push lake metabolic balances further into heterotrophy (Klug et al., 2012; Sadro et al., 2011; Tsai et al., 2008), either by decreasing surface primary production through lower water transparency or by stimulating bacterial respiration through addition of labile, terrestrial organic matter (Johengen et al., 2008; Ojala et al., 2011; Vachon and Giorgio, 2014). Considering the size of Lake Geneva, it is unlikely that floods may affect the whole ecosystem metabolism (Vachon and Giorgio, 2014). Yet, since riverborne intrusions are rich in organic matter, they could locally be hotspots for bacterial respiration that would counteract the net oxygen inputs in the hypolimnion. In this metabolic hypothesis, riverborne intrusions could cause a null or even a negative effect on hypolimnetic oxygen concentrations.

The overarching aim of this paper was, therefore, to study the net oxygen effect of flood driven riverborne intrusions in Lake Geneva. The study combined direct observational data collected during an extreme flooding event in May 2015, while the lake was already stratified, supported with an experimental test designed to evaluate the consequences of river water inputs on the hypolimnetic respiration.

2 Materials and methods

2.1 Field survey

Lake Geneva is the largest lake of Western Europe in terms of volume (89 km^3), and one of the deepest (309 m). 84 % of the water input originate from the two main rivers, the Rhône (75 %) and the Dranse (9 %), both flowing into the eastern basin. The river discharge and water quality are continuously monitored by the FOEN (Federal Office for the Environment, Switzerland for the Rhône), the DREAL (Direction Régionale de l'Environnement, de l'Aménagement et du Logement, for discharge of the Dranse River http://www.hydro.eaufrance.fr/stations/V0334010) and the Observatory of Alpine Lakes, respectively (for the water quality of the Dranse, http://www6.inra.fr/soere-ola). Discharge (hourly record) and water quality (two-weeks integrated sample) of the Rhône River are monitored at Porte-du-Scex FOEN station, 6 km upstream of the Rhône inflow. Discharge of

the Dranse is recorded at the Reyvroz hydrological station, 20 km upstream of the Dranse inlet to Lake Geneva, while water quality surveys are performed close to the river delta.

The Rhône river hydrological regime was originally of a typical glacier-type but exploitation of the river flow for hydro-electrical production has substantially smoothed the seasonal variability of water discharge over the latest 40 years. Summer discharges are currently only twice those observed in winter (Loizeau and Dominik, 2000). The average annual discharge at Porte du Scex in May over 1935-2013 was 208 $m^3 s^{-1}$. The Dranse, which is the second most important tributary of Lake Geneva, has a typical nival flow regime (Meybeck et al., 1991), with a maximum discharge in May (average discharge in May over 1906-2003: 39 $m^3 s^{-1}$).

The consequences of the heavy rain of 1-5th May 2015 on physico-chemical lake properties were investigated through a specific lake survey. 24 sites were sampled within one day (May 7th 2015) with a multi-parameter profiler (Sea&Sun Technology, CTD-90 multi-parameter probe), which includes measurements of depth, temperature (T), conductivity, turbidity (Tu) and dissolved oxygen concentration (O_2). The O_2 oxyguard (Clark type) is regularly calibrated with a long term stability optode (Anderaa 4330F) but, in the present study, no drift in the O_2 measurements was expected during a single day survey.

The 24 sampling sites cover an area of ~200 km^2 over the Eastern basin. The sampling design was specifically intended to sample the influence of the two main rivers and to investigate the local influence of deep intrusions on O_2 concentrations. For this reason, all sites were chosen with a local depth largely exceeding 100 m. Particular care was taken to encompass the main active sub-lacustrine canyons of the Rhône and of the Dranse, as well as their surroundings, and therefore to optimize the chance to probe intrusion plumes. The high resolution CTD survey provided spatial information of O_2, Tu and T. Maps of hypolimnetic properties were constructed with krigging interpolation method.

The net effect of river intrusion on the dissolved oxygen concentration was quantified by comparing the O_2 profile within the intrusion layer to a theoretically-observed linearly decreasing O_2 profile within this layer as typically observed in intrusion-free (undisturbed) CTD profiles.

2.2 Oxygen consumption experiment

In order to test whether inputs of riverine organic carbon within the lake hypolimnion could drive significant oxygen consumption via microbial respiration, an incubation experiment was

conducted in October 2015. On Oct 19th, 15 L of Lake Geneva hypolimnetic water were collected with a VanDorn bottle from 100 m and 200 m depths at SHL2, such as 20 L of water from the Dranse, at less than 1 km from its entrance into Lake Geneva. One litre of lake and river water was kept in a glass bottle for further analyses of Carbon (C), Nitrogen (N) and Phosphorus (P) contents. Concentrations in total and dissolved organic C (TOC, DOC) were measured with/without filtration on Whatman GF/F filters (0.7 μm nominal pore size), on a TIC/TOC analyser (OI Analytical). Nutrients were analysed by standard colorimetric methods (Association Française de Normalisation, 1990).

Pure lake and riverine waters, and mixed waters, in which different percentages of lake water were substituted by riverine waters, were incubated in 280 mL hermetically-closed glass-bottles equipped with SP-PSt3 planar oxygen-sensitive spots (PreSens), according to the experimental design presented in Table 1. Tested range of dilution of riverine waters in lake hypolimnion was designed based on bulk estimated values of river mixing in Lake Geneva (see Appendix A1). Triplicates of each sample were incubated in a temperature-controlled dark chamber at 10 °C (a realistic temperature for river and hypolimnetic conditions during the flood). Changes in O_2 over time were measured using a PreSens Fibox 3 equipped with a fiber optic oxygen transmitter. Initial O_2 concentrations were measured 1-hour after the start of the incubation, once water temperature had stabilized at 10 °C. Thereafter, O_2, and corresponding oxygen consumption, was measured once or twice per day for four days. Calibration of the Pre-Sens (two-point calibration at 0-100% oxygen saturation) was tested again at the end of the experiment (<1 week) and showed no drift over the whole duration of the bioassays Results were analysed by ANCOVA using O_2 consumption as the response variable, treatment as the factor, and time as covariate, including interactions. Further comparisons between treatments or specific dates were performed using Student's T test or Kruskal Wallis tests in cases of heterogeneous variances.

3 Results

3.1 Field survey

For the 2015 spring flood events, heavy rainfalls over the Lake Geneva watershed started on May 1st until May 4th (total rainfall > 100 mm over these four days). For comparison, this is a record for the City of Bex (Switzerland), located 20 km upstream of Lake Geneva along the Rhône River, that had last been observed in December 1916. The discharge of the Rhône

increased from ~140 $m^3 s^{-1}$ at the end of April up to a maximum of 504 $m^3 s^{-1}$ on May 5th (Fig. 1a). This discharge reached the 98th percentile of the cumulative distribution of the Rhône discharges over 1976 - 2009, and corresponded to an annual return time of the Rhône floods at the entrance of Lake Geneva (Fig. 1b). The Rhône water temperature was 8 °C and O_2 concentrations were 11 $mgO_2 L^{-1}$ (data source: FOEN, Switzerland). On the sampling date (May 7th), the Rhône discharges remained elevated with a daily average of ~ 400 $m^3 s^{-1}$.

The heavy rainfalls of early May 2015 increased the flow of the Dranse, which was already at its seasonal maximum, concurring in generating a flood of exceptional amplitude. Between April 30th and May 4th, the discharge increased from 26 to 300 $m^3 s^{-1}$, right before the monitoring station collapsed (Fig. 1a). This was a new record exceeding the previous historical maximum discharge ever recorded at the Dranse hydrometric station (229 $m^3 s^{-1}$ on September 22nd 1968). The estimated return time of the 2015 flood event for the Dranse was 50 years (Fig. 1c). The flooding waters were highly turbid with a concentration of suspended matter reaching > 2000 mg L^{-1} (averaged concentration of 18 mg L^{-1} in 2014; data from the observatory of large lakes, France). The suspended organic matter concentration was 195 mg L^{-1} (annual average of 5 mg L^{-1} in 2014). DOC was twice the average annual concentration (2.3 vs 1.2 mgC L^{-1}). Dissolved nutrient concentrations were moderate (PO_4^{3-} = 10 µgP L^{-1}; NO_3^- = 480 µgN L^{-1}). Although not regularly monitored, the highly torrential flow of the Dranse suggests saturated oxygen concentrations.

The flood inflows are highly turbid as compared to Lake Geneva waters (< 5 FTU) and turbidity was thereafter used as a tracer for intrusive waters within the lake. CTD profiles for all surveyed stations are provided as Appendix data (Figure A2). Of the 24 sites, more than 50 % had hypolimnetic turbidity peaks attributed to river intrusions (Fig. 2). The use of turbidity as a proxy for riverborne waters was also validated by temperature profiles showing a consistent increase of temperature in the turbid layers and thereby indicating that, locally, the density of the water was significantly affected by suspended matters and not anymore a function of temperature and salinity only (see A2). This trend is clearly noticeable in BP18 located within the far Dranse underflow (Fig. 3a and b). The turbidity signal from the Rhône was restricted to the few stations located less than 2 km downstream (BP8 and 9), while the turbidity current from the Dranse penetrated much further within the lake, even reaching the reference monitoring station (SHL2 = BP18), 6 km downstream. The two northernmost stations BP2 and 3 were within the small but noticeable underflow of the Veveyse River

(Figure 2). Except for the stations closest to the Rhône (BP8) and Dranse (BP21, 22 and 25), the underflow was split between two different hypolimnetic layers: a very turbid underflow within the lower hypolimnion (below 110 m, BP5, 7, 9 and 13 for the Rhône underflow, BP16 and 18 for the Dranse River), and less turbid underflow between 50 and 110 m depths (BP2 and 29).

Undisturbed profiles typically indicated a similar trend in O_2 slope ($\Delta O_2/\Delta depth$ = -0.022 mg L^{-1} m^{-1}, SD 0.006 mg L^{-1} m^{-1}, based on 9 profiles, BP13, 4, 6, 11, 12, 14, 19 and 28, Figure A1) in the lower hypolimnion defined as the region below the winter deep mixing maximum (110 m) and the layer of influence of the bottom (20 m above the sediment interface). The winter deep mixing maximum at depth 110 m was also confirmed by a CTD profile carried out one week earlier by the Observatory of Alpine Lakes, France (not shown). Although more contrasted, the upper hypolimnion, i.e. between the thermocline depth and the winter deep mixing depth (Fig. 2b), was characterized by a less steep O_2 slope (e.g. the upper hypolimnion had mixed three months earlier).

The net effect of the intrusion on the O_2 was first assessed by comparing intrusion-affected and nearest intrusion-free CTD profiles (Fig. 3). Surprisingly, at no sampling site did the turbidity peak match with a local maximum in O_2 that could compare to the lens anomalies reported by Meybeck et al. (1991). Instead, the depths of the turbidity peak coincided with a disruption of the background decreasing trend in O_2 as a function of depth, clearly noticeable for instance in the comparison of the O_2 profiles at BP18 (affected by the Dranse) and BP16 (not affected, Fig. 3a and b). Such a reduction of O_2 vertical gradients as recorded at BP5, 8, 9 and 18, suggests the formation of a mixed layer due to the increased momentum within the underflow. Depth-averaged O_2 in the interval 30 to 270 m at BP16 and BP18 were identical (7.0 mgO_2 L^{-1}) and, thereby, supported the hypothesis that the studied intrusion and related extreme flood event had no net effect on the O_2 concentration but rather efficiently mixed turbid-affected hypolimnetic layers. Although the trend was not as clear as in the middle of the lake, similar conclusions arose from the comparison of CTD profiles carried out near the Rhône at BP8 and BP12 (Fig. 3b and c). More information on the Rhône intrusion is provided as Appendix data (Figure A3).

At stations BP2, 3, 21, 22, 25, and 29, turbid layers above 110-m depths even coincided with a decrease in O_2 concentration. The drop in O_2 at BP2 in the turbid layer between 58 m and 86 m is a stunning example with a decrease in O_2 of ~0.3 mg L^{-1}. O_2 concentration decline within

turbid layers was also observed near the Dranse at BP21, 22 and 25 (Fig. 4). Although all three stations were affected by the Dranse underflow, turbid intrusion was observed at different depths. While O_2 of the three stations was highly comparable at depths unaffected by the turbid flow (15 - 50 m), their O_2 profiles diverged at depths affected by the turbidity current. Below 50 m, O_2 concentration at BP21 dropped as the turbidity increased, while O_2 concentration at BP22 and BP25 remained higher and similar between 50 m and 70 m. Below 70 m, O_2 concentration at BP22 dropped as turbidity increased and last, the turbidity intrusion at 90 m depth in BP 25 coincided with the collapse of the three O_2 profiles (e.g. O_2 drop at BP25). Surprisingly, below 110 m, O_2 profiles remains similar at the three stations independently of turbidity values.

The difference in depth-averaged O_2 between measured profile and associated linear fit through the turbid layer provided a first order parameterization of the net O_2 effect of the intrusion. The spatial heterogeneity in large systems impede from defining a single reference profile valid for the entire lake. Furthermore, the change in O_2 slope at the winter deep mixing maximum (110 m) precluded the use of this linear fitting method for any intrusion encompassing this layer (i.e. BP 21, 22 and 25) although they clearly showed evidence for oxygen depletion within the turbid layer (see above). We therefore restricted this analysis to intrusions located in the upper part of the hypolimnion (between the thermocline and the winter deep mixing maximum) or intrusions located below this winter deep mixing maximum. Relative changes in O_2 in the turbid layers flowing within the lowest hypolimnion (> 110 m depth) were not significant (-0.07 mg L^{-1}, SD 0.05 mg L^{-1}, t = -2.50, df = 4, p-value = 0.066 ; Fig. 6). Net oxygen effects associated turbid layers flowing within the upper hypolimnion were more variable (-0.19 mg $L^{-1,}$ SD 0.16 mg L^{-1}), but they were, on average, significantly negative (t = -3.68, df = 7, p-value = 0.007), attesting of an actual oxygen debt at these shallower depths.

3.2 Oxygen consumption experiment

The experiment was designed *a posteriori* in order to explain observed differences in the oxygen net effect of the Dranse intrusion between the upper and the lower hypolimnion (above and below 110 m depth). In October 2015, DOC concentrations in the lake hypolimnion and in the river were very similar (0.80 mgC L^{-1} at 100 m depths, 0.70 mgC L^{-1} at 200 m depths and 0.75 mgC L^{-1} in the Dranse waters). Particulate organic carbon concentrations were low (< 0.10 mgC L^{-1}). DOC in the Dranse waters during the experiment

were about three times lower than those observed during the flood but, more importantly, DOC concentrations were highly comparable between dilution conditions. As a result, differences in O_2 consumption between treatments cannot be driven by initial differences in carbon contents. Standardizing consumed O_2 by amount of initial organic carbon was not necessary.

Dissolved nutrient concentrations were very low in the Dranse at the time of collection. Orthophosphate concentrations were half those recorded during the flood (5 µgP L^{-1}) while nitrate concentrations were more similar (580 µgN L^{-1}). Orthophosphate concentrations at 100 m and 200 m depth were very comparable to those recorded during the flood (13 and 29 µgP L^{-1} respectively at both dates) while nitrate concentrations were slightly lower (620 and 560 µgN L^{-1} in October, compared to 670 and 630 µgN L^{-1}, in May 2015).

Initial O_2 concentrations were not different between incubation treatments and ranged between 8-10 mgO_2 L^{-1}. Beyond 86 or 92 hours of incubations, some treatments (D100%, L200-100%, L200-99%) presented a second phase of increased oxygen consumption that indicated the start of nitrification processes, i.e. oxygen consumption independent from aerobic mineralization. In order to avoid any potential bias due to nitrification, final oxygen consumption values are considered at 86 h of incubation. O_2 consumption after 86h was significantly different between treatments (ANCOVA $F_{7,64}$= 27, $p < 2.10^{-16}$) and time ($F_{2,64}$ = 21, $p = 9.10^{-10}$), with a high consumption rate within the first 20 h, and a relative stabilization thereafter (Fig 6, a b).

O_2 consumption was the highest for the Dranse water, reaching 2.6 mgO_2 L^{-1} after 86 h, while final values of O_2 consumption were significantly lower for the lake waters. Within lacustrine waters, O_2 consumption was higher at 200 m than 100 m depths (1.0 mgO_2 L^{-1} and 0.7 mgO_2 L^{-1} respectively, Kruskal Wallis χ^2= 4.0, *p = 0.04*).

Dilution of Lake Geneva water at 200 m depth by riverine water (L200-100%, L200-99%, L200-90% and L200-50%) did not significantly affect the dynamics of O_2 consumption over time (ANCOVA, $F_{treatment\ 3,84}$ = 2.0, p = 0.10, Fig 6a. and c). O_2 consumption between treatments were therefore not significantly different after 15 h or beyond of incubation of 200 m deep water. Observed consumption values were similar to those expected from a linear mixing model. For the 50/50 treatment, consumption was even significantly lower than those expected. In contrast, O_2 consumption in lake water collected at 100 m depths was higher for a treatment with 1-10% of riverine water added, as compared to the non-diluted samples

(ANCOVA, $F_{treatment\ 2,66} = 96$, $p < 2.10^{-16}$). From 15 h of incubation and beyond, O_2 consumption in samples incubated with 1-10% of riverine water was significantly (25 - 150%) higher than for undiluted samples, although initial carbon content was similar between all treatments (Fig. 6b). Observed consumption values after 86 h exceeded by 60% those expected from a linear mixing model in both treatments (Fig. 6c).

4 Discussion

4.1 River intrusions during the flooding event

Considering the extreme intensity of the observed rain event and subsequent river discharges, we expected the flood-induced turbidity current to be heavy enough to trigger an underflow along the lake bed and therefore reach the deepest layers of the water column. However, no clear signatures of a bottom following underflow could be observed for this specific event. We estimated the sediment load in the Rhône river during the flood event by fitting the relationship between river discharge, Q, and sediment load, C with a power law $C = aQ^b$ as suggested in Loizeau and Dominik (2000) and Mulder et al. (2003). Our best fit for the 50 years of measurements resulted in $a = 5.7 \times 10^{-4}$ and $b = 2.36$ (see Appendix data, A4) which is in good agreement with previously estimated relationships (Loizeau and Dominik, 2000). Based on this relationship, the resulting estimated sediment load at the flood paroxysmal phase reached 1.4 kg m^{-3} (or g L^{-1}). Assuming that the sediment load was predominantly made of Quartz ($\rho_{sed} = 2700$ kg m^{-3}), the density of the Rhône river was estimated as $\rho_{R,tot} = \rho_w(S, T) + (1-\rho_{sed} / \rho_w(S, T))\ aQ^b = 1000.7$ kg m^{-3}, where $\rho_w(S, T)$ is the density of the water depending on the temperature and salinity (Chen and Millero, 1986). This value was slightly lower than the density of the lake water at the deepest location (1001.4 kg m^{-3}) and did not account for the later entrainment of lake water into the intrusion. Similar estimates for the Dranse provided $\rho_{R,tot} = 1001.2$ kg m^{-3} assuming the same river temperature than for the Rhône. Similar first order calculation suggests that the lower part of the intrusion stopped at ~160 m for Rhône water and at ~250 m for Dranse water, which is in very good agreement with the observations. Our results therefore confirm that a Rhône discharge with annual return time is actually plunging. However, the underflow may find its equilibrium density in the hypolimnion and further evolve as an intrusion, rather than a true hyperpycnal current, for which much higher discharges are required. Recent observations of a thick turbidite in Lake

Geneva sedimentological patterns were, for instance, interpreted as the result of a major underflow and resulting landslides in October 2000 (Corella et al., 2014) with an extremely strong Rhône discharge of nearly 1400 m^3 s^{-1} (return time 300 years) and a sediment load of > 9 kg m^{-3}. Hence, although Lambert and Giovanoli (1988) recorded 11 underflows associated with elevated or rapidly changing discharge in the Rhône canyon, ~2.5 km away from the river mouth over a short three months period in summer 1985, we could not time-correlate any of these underflows to any of the O_2 anomalies studied in the same year in the deepest 50 m of the lake (269 - 309 m) by Meybeck et al (1991) (see Bouffard et al., 2016). This suggests that none of these underflows were ultimately strong enough to travel far into the lake. Alternatively the previously postulated relationship between O_2 anomalies and Rhône underflows as suggested by Meybeck et al. (1991) is questionable as our observation shows that a one-year return time discharge rate triggers a plunging underflow that will quickly degenerate into a deep intrusion. Underflows evolving up to the centre of the lake require strong discharge with return times longer than one year and are therefore infrequent. Due to its closer location to the lake centre, the Dranse is more likely to affect the lake centre (BP18, SHL2) with interflow (present study) or underflow (Meybeck et al. 1991). Note also that Meybeck et al. (1991) remained inconclusive regarding the exact cause of the observed deep underflow. Besides river inflow, the authors also suggest the influence of winter cooling and subsequent along slopes oxygen-rich density current as other plausible mechanism. Apparent discrepancies between observed patterns and Meybeck et al. (1991)'s hypotheses are further discussed in Bouffard et al (2016).

4.2 Consequences of river intrusions on hypolimnetic oxygen concentrations

Overall, the dataset presented herein rejected the hypothesis of a net oxygen gain due the river intrusions in Lake Geneva during this important flooding event.

When comparing our results to those that supported this original hypothesis, it seems that the net effect of river intrusions on hypolimnetic oxygen concentrations of Lake Geneva varies depending on the properties of the intrusion flow. In May 2015, neither the Dranse nor the Rhône generated an underflow plunging to the lake bottom and we cannot exclude that such hyperpycnal flows could indeed contribute to deep water oxygen replenishment. Instead, we observed two types of intrusions, i.e. in the upper hypolimnion that had been previously mixed during the preceding winter, and in the lower hypolimnion. Intrusions in the lower hypolimnion acted essentially through their mixing momentum and partly redistributed

oxygen within the mixed layers with, yet, no net benefit. Intrusions above 110 m depths consistently generated local oxygen depletion. Before the flood, O_2 concentrations in the upper hypolimnion were higher than in the lower hypolimnion (9.5 $mgO_2\ L^{-1}$ and < 7 $mgO_2\ L^{-1}$ respectively) because the winter mixing did not reach deeper than 110 m that year. The O_2 concentrations in the Rhône were as high as 11 mg L^{-1} and we assumed that the Dranse waters were also saturated. It is then unlikely that the observed oxygen depletion in the turbidity current observed in the upper hypolimnion directly resulted from intrusions of O_2-depleted river waters. Instead, they point to increased oxygen consumption in the uppermost turbidity current, for which the metabolic consequences of the riverborne inputs would have taken over its physical, mixing effect.

These observations suggested (i) that respiration of diluted, riverborne organic matter in the hypolimnion had a significant effect on oxygen concentrations and (ii) that the contribution of respiration varied between the upper and lowermost hypolimnion. The oxygen consumption experiment that we designed, *a posteriori*, aimed at testing whether such assumptions were reasonable. Although O_2 and DOC concentrations in the hypolimnetic waters were likely to be relatively similar in October to those right before the flood, they were undoubtedly quite different for the river waters. However, this experiment did not intend to mimic conditions during the flood but instead to investigate the metabolic processes in the different hypolimnetic layers.

4.3 Hypolimnetic respiration of riverborne organic matter

Bioassays intended to test for the possibility of fast and efficient respiration of riverborne organic matter in the lake hypolimnion as suggested by the field data, such as for depth-related differences in the metabolic processing of this organic matter. Ideally, the experiment should have been conducted during the studied flooding event but the available background literature at the time of study pleaded for a refractory nature of allochthonous organic matter, hampering fast and significant metabolic processing within the lake. The flood we had been studied was of exceptional amplitude (a 50-yr return time at least for the Dranse river) and was not likely to occur one more time soon. The point of the bioassays was then to investigate the processes underlying the observed field results, and we were lucky enough that even for different flowing conditions, bioassays results reflected very well the field conditions. This stresses out the fact these processes might not be exceptional, instead their overall contribution to the lake O_2 budget gets more significant in flowing conditions.

Microbial respiration rates for the Dranse water were initially three times those of the lake hypolimnetic waters, for similar DOC concentrations. In order to best reproduce processes occurring during the river intrusion in the lake, we did not filter water to remove plankton before incubations, in contrast to experiments aiming at separating bacterial and planktonic respiration rates (Warkentin et al., 2007). It is therefore likely that the respiration was higher in the Dranse water samples because it included both bacterial and autotrophic planktonic components compared to samples from the dark hypolimnetic layers in which the sole microbial heterotrophs shall be present.

However, considering a respiratory quotient of 0.82 (Williams and del Giorgio, 2005), consumed O_2 in the Dranse river samples after 86 h would correspond to the oxidation of 0.75 mgC L^{-1}, i.e. > 90 % of TOC. These values of short –term oxygen consumption rates belong to the upper end of the range reported for lakes and streams by Berggren et al. (2012). They attest of an important short-term labile pool of DOC (*sensu* Guillemette and del Giorgio, 2011) in the river waters (low-molecular weight, relatively young DOC, Agren et al., 2008) but also of low bacterial growth efficiency due to nutrient limitation in the oligotrophic conditions of the Dranse rivers (Cimbleris and Kalff, 1998; Wiegner and Seitzinger, 2004). River water samples were collected for the experiment purposes at times of moderate hydrological loads and DOC as well as phosphate concentrations in the river during the flood were much higher suggesting fast leaching of the watershed soils (Agren et al., 2008). It is likely that river DOC during the flood was even more labile, since it was mobilized and transported by rapid flush and fast transport of soil organic matter (Agren et al., 2008; Bergström and Jansson, 2000).

In contrast, respiration recorded in the lake hypolimnetic waters corresponded to lower oxidation rates (23 % and 42 % of TOC at 100 m and 200 m depths, respectively) for similar initial organic carbon contents. Bacterial growth (including respiration, production, and growth efficiencies) depends both on nutrient limitation and organic matter quality (Farjalla et al., 2009). At these depths, microbial metabolism is less likely to be nutrient limited but bacterial abundances are nevertheless usually low (around 10^5 cells ml^{-1}, S. Jacquet, pers. comm.) suggesting low values for bacterial production. Besides, hypolimnetic waters of Lake Geneva have long-residence times (time of ~20 years, Meybeck, 1970) and although most of the lakes' hypolimnetic DOC might primarily originate from autochthonous primary production, DOC aging through microbial reworking contributes to increasing its aromaticity

(Berggren et al., 2009) resulting in low bacterial growth efficiencies even without nutrient limitation (Berggren et al., 2009). In that case, lower respiration values for hypolimnetic waters suggested that lake DOC was semi-labile as compared to the Dranse DOC that might be fresher and more readily available.

Nevertheless, higher oxygen consumption rates measured for the lowermost hypolimnion as compared to its upper layer are surprising at first sight as they point to a higher availability for lake DOC of greater depths. Such depth–related differences in C availability for microbial metabolism are also consistent with the substitution assays showing that riverborne, labile DOC inputs stimulated microbial respiration only for the supposingly C-limited samples, i.e. the 100m depth lake water (Eiler et al., 2003). If DOC had the same sources in both hypolimnetic layers, the greater water retention time would instead contribute in decreasing DOC bioavailability with depth. Yet, DOC concentrations increases between the lower limit of the mixed hypolimnion (110 m) and the lake bottom (309 m), from 0.7 to 0.8 mgC L^{-1}, as a likely consequence of DOC remobilization from the sediment and accumulation in the overlaying water column (Gonsior et al., 2013). Recent studies highlighted DOC release from the sediment is a substantial source of labile DOC to the water column (Downing et al., 2008), which could increase to the short-term labile pool of DOC in the unmixed hypolimnion. While additional investigation on deep DOC quality would be required, fluxes of sediment DOC to the unmixed deeper hypolimnetic layer could sustain higher respiration rates as compared to the most superficial one for which microbial metabolism is the most limited by organic matter quality.

More surprisingly though, the stimulation of microbial respiration for the 100-m depth treatment was disproportionate as compared to the quantity of added labile OC. The substitution of 1-10 % of lake DOC by riverborne, more labile DOC led to respiration exceeding by 60% values that would be expected from simple mixing models of single source yields. Similar overyield respiration effects were documented by Farjalla et al. (2009) who observed that a mixture of fresh and aged DOC acted synergistically on the bacterial respiration rate (Farjalla et al., 2009) resulting in disproportionately increased rates compared to single substrates. We did not filter the Dranse water to remove microbes prior to incubations, with the purpose of more closely replicating realistic conditions within turbidity currents, and it is likely that we added an inoculum of river microbes to the mixture experiments. Increased respiration of particulate carbon would have been an explanation in

the case that the riverine water was rich in POC. However, for both lake and river waters, POC concentrations were basically beyond detection limits (<0.1 $mg.L^{-1}$) and, as for DOC, do not account for the excess oxygen consumption. A greater microbial diversity in the mixture samples could also favor co-metabolism on carbon compound decomposition and therefore the observed overyielding, as suggested by Farjalla et al. (2009). Yet, more recent investigations revealed that the initial microbial community composition has less impact on DOC use than the nature of DOC itself (Attermeyer et al., 2014). The microbial riverine inoculum might then not account for the totality of the enhanced decomposition of DOC in the mixture, while metabolic synergies in the microbial use of the different DOC qualities could also be involved (Fonte et al., 2013).

4.4 Experimental and observational conclusions on the effect of river intrusion on the hypolimnetic oxygen concentrations of Lake Geneva.

The May 2015 flood episodes did not trigger true underflow processes. Therefore, we cannot generally exclude that underflows, in which very high turbidity limits the mixing of the water masses of the river and the lake, can finally replenish deep water oxygen. However, rough estimations confirmed that such truly underflow processes are far more rare than previously thought. Exceptional events that indeed replenish oxygen at the bottom of the lake might occur at decennial, rather than annual time scales. Our observations pointed to null or negative effect of river intrusions on the deep water oxygen content of Lake Geneva. Rather than increasing deep water oxygen concentrations these intrusions cause physical mixing of the deep hypolimnion, i.e. redistributing oxygen over depth, or have a metabolic effect at least at the temporal scale at which we observed the process (i.e. 3 days after the discharge peak). It is likely though that these patterns may have followed a temporary and even shorter-lasting increase in oxygen in the intrusion within the first hours of the event. The final consequences on the benthic biota are unclear since the effect on O_2 might be transient and shall not persist for long within the lake hypolimnion. Indeed, the change in the deep hypolimnion O_2 profiles due to the homogenization by the intrusion was poorly visible during the monitoring survey performed at SHL2 a few days after the end of the flooding event (11 May, data not shown). The mechanisms by which river water intrudes both above and below the deep mixing layer remain to be investigated, such as for the associated differences in the metabolic fate of riverborne organic matter. Nevertheless, our observational survey and bioassays highlighted that these intrusions provide interfaces where riverine and lake organic matter are mixed and

can act as biogeochemical hotspots. The quantity of substituted DOC does not account for the excess oxygen consumption observed in the L100-99% and L100-90% treatments. Fertilization and nitrification effects, such as respiration of particulate organic matter, could be reasonably ruled out in both the field survey and bioassays. Instead, our results suggest that more of the lake DOC, from intermediate hypolimnetic depth, had been respired as a small fraction of more labile, riverborne, DOM was substituted. Even if the role played by a potential inoculum of riverine microbes cannot be ruled out, river intrusions in the upper hypolimnion resulted in an increase of autochthonous organic matter respiration. This mechanism by which a small addition of labile organic matter stimulates the mineralization of less available organic matter is referred as to 'priming effect'. Priming effect has been thoroughly investigated in soils but evidence are still sought in aquatic systems (Bianchi, 2011; Catalán et al., 2015). River plumes had been identified as sites prone to host priming effect, since they shall bring in contact different sources of organic matters with varying quality (Bianchi, 2011; Guenet et al., 2010). Even though several papers, along with the present results, have revised the long-standing hypothesis of the recalcitrance of terrestrial organic matter (Guillemette and del Giorgio, 2011; Roehm et al., 2009), investigations of aquatic priming effect are still based on the hypothesis that lacustrine OM shall be the primer and terrestrial OM the "primed" (Catalán et al., 2015). In the present study, the vertical consideration of the intrusion challenged our preconceived thoughts on the quality of aquatic DOC, showing that lacustrine DOC was semi-labile, but of heterogeneous quality with depths, while river OM was potentially acting as the primer. Even though formal demonstration of priming effect will deserve further evidence, our in-situ and ex-situ observations suggest that deep river intrusion in Lake Geneva could be potential hotspots for aquatic priming, fostering the mineralization of deep, less labile lacustrine organic matter.

Appendix

A1. Estimated values of river mixing in Lake Geneva

A2. CTD profiles

A3. CTD transect from the Rhône mouth to the lake centre. These series of CTD profiles suggest that the net O_2 effect of the Rhône intrusion is limited or null but instead efficiently homogenized the O_2 in the hypolimnetic water affected by the intrusion (reduction of the O_2 gradient close to the Rhône River). Intrusions are associated with elevated Tu signal.

A4. Sediment rating curve of the Rhône River at La Porte-du-Scex from 1964 to 2015. Best fit Concentration [mg L^{-1}] = aQ^b, with Q = discharge [m^3 s^{-1}], yields a = 5.7 x 10^{-4} (3.1 x 10^{-4}, 8.3 x 10^{-4}) and b = 2.365 (2.29, 2.441) with the 95% confidence interval in parenthesis.

A5. GPS coordinate (geodetic datum CH1903+) of the CTD profiles carried out on May 7th 2015

Author contribution

Both authors contributed equally to the field work, the data analysis and the redaction of the manuscript.

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Figures captions

Fig. 1. Hydrological characteristics of the flooding event of May 2015. a. Daily precipitation and discharges of the two dominant tributaries of Lake Geneva, the Rhône and the Dranse rivers over the months preceding and following the flood. The break in the discharge record of the Dranse corresponds to the date at which the station collapsed. Cumulative distribution of the Rhône discharges in 1976-2009 (b) and Dranse discharges 1957-2014 (c). Red lines indicate the maximum discharges of the May 2015 event.

Fig. 2a. Spatial distribution of maximum hypolimnetic turbidity (40 - 300 m depth) as a tracer for flooding river intrusions. Identified stations are those for which profiles were provided in Figure 3b. The inserted figure shows typical temperature and O_2 profiles for an undisturbed station. Note the linear decrease of O_2 with depth in the lower hypolimnion (below the deep winter maximum). GPS location of the CTD profiles is indicated in the Appendix information (A5).

Fig. 3. Comparison of temperature, turbidity and O_2 depth-profiles for nearby stations, one being undisturbed (dotted lines), and the other highly disturbed (continuous lines) by the turbidity current of the Dranse (a,b); the Veveyse (c,d) and the Rhône rivers (d,e,).

Fig. 4. Comparison of turbidity (a) and O_2 (b) depth-profiles for the three stations close to the Dranse river mouth. The shaded area corresponds to the upper hypolimnion, i.e. water layers that have been mixed during the preceding winter.

Fig. 5. Net effect of the turbidity layer on O_2 concentrations calculated for intrusion above (n=8) and below (n=13) the deep winter winter maximum (110 m).

Fig. 6. O_2 consumption in the bioassays. a. Bioassays conducted for the lake water collected in the lowermost hypolimnion at 200m depth (100% 200 m), and with 1, 10% and 50%

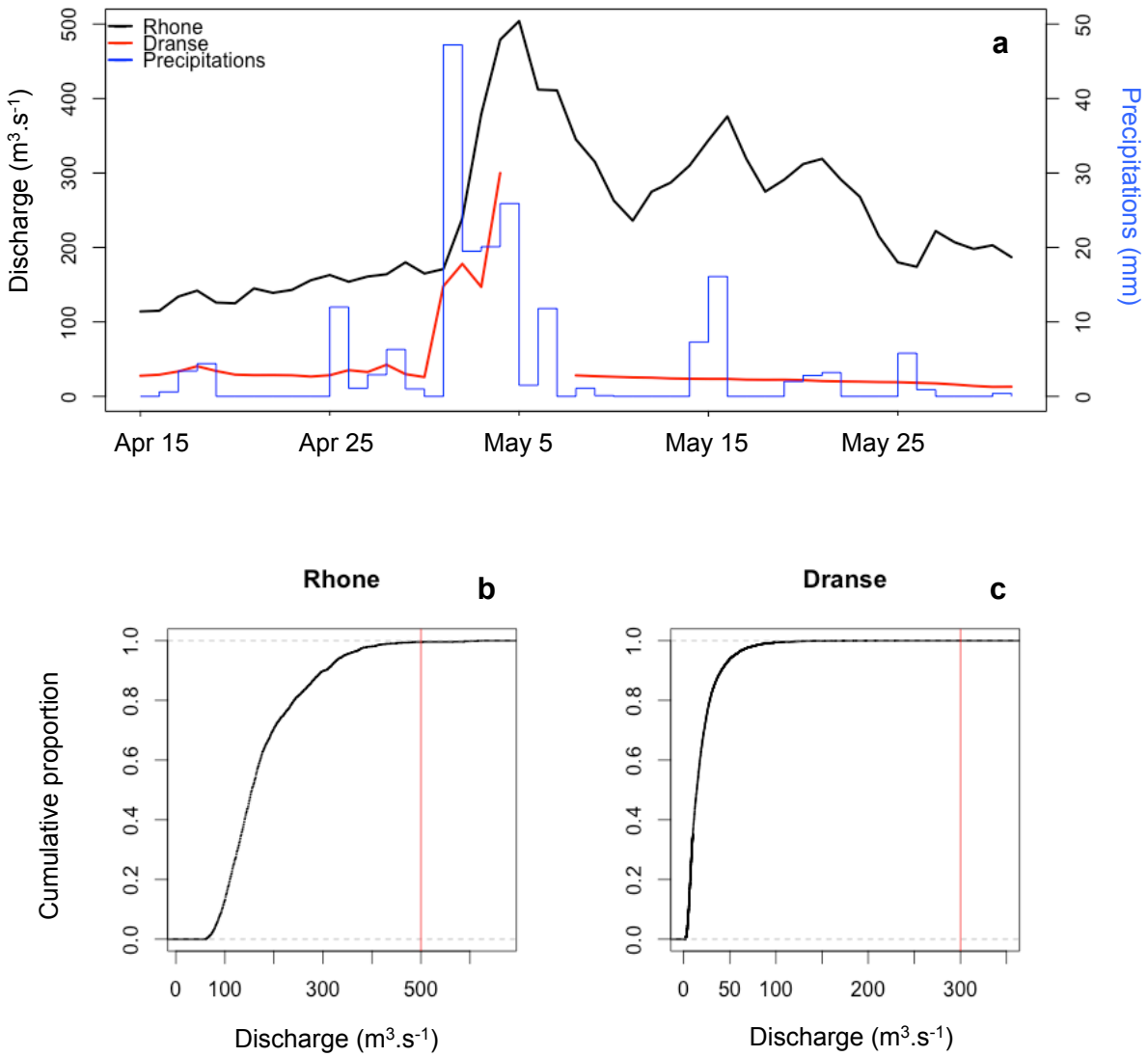
substitution, respectively, with Dranse water (99% 200 m, 90% 200 m and 50% 200 m, respectively, and compared for Dranse water only (D 100%). b. Bioassays conducted for the lake water collected in the uppermost hypolimnion at 100 m depth (100% 100 m), with 1 and 10% substitution, respectively, with Dranse water (99% 100 m, 90% 100 m respectively), and compared for the Dranse water (D 100%). c. Expected (based on a linear mixing model) and observed (average ± SD on triplicates) O_2 consumption values after 86h-incubation of mixed lake and riverborne waters. Specified p-values correspond to the outputs of the Student's tests comparing observed and theoretical, expected consumptions.

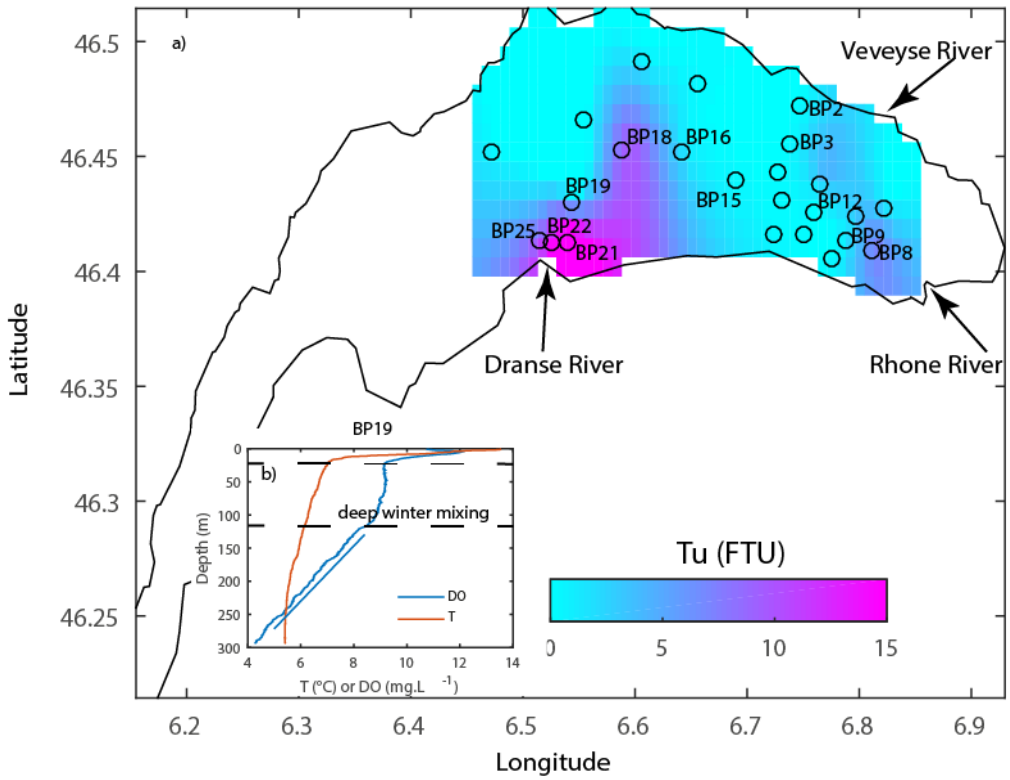
Table 1. Design of the incubation experiment.

Sample designation	Percent composition Lake Water		
	200m-depth lake water	100m-depth lake water	Dranse water
L200-100%	100%		
L200-99%	99%		1%
L200-90%	90%		10%
L200-50%	50%		50%
L100-100%		100%	
L100-99%		99%	1%
L100-90%		90%	10%
D-100%			100%

Figures

Figure 1





1

2 Figure 2

3

4

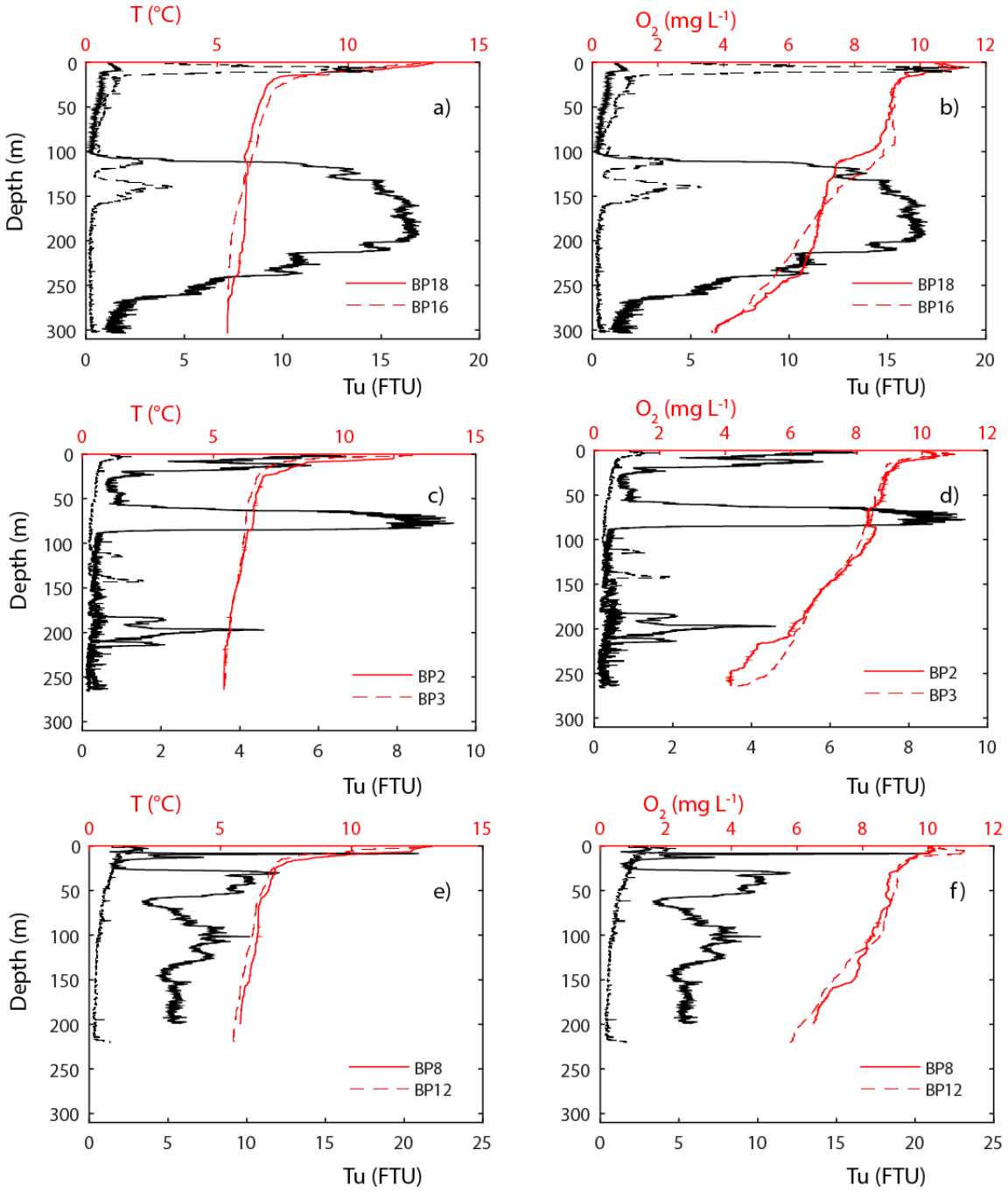


Figure 3

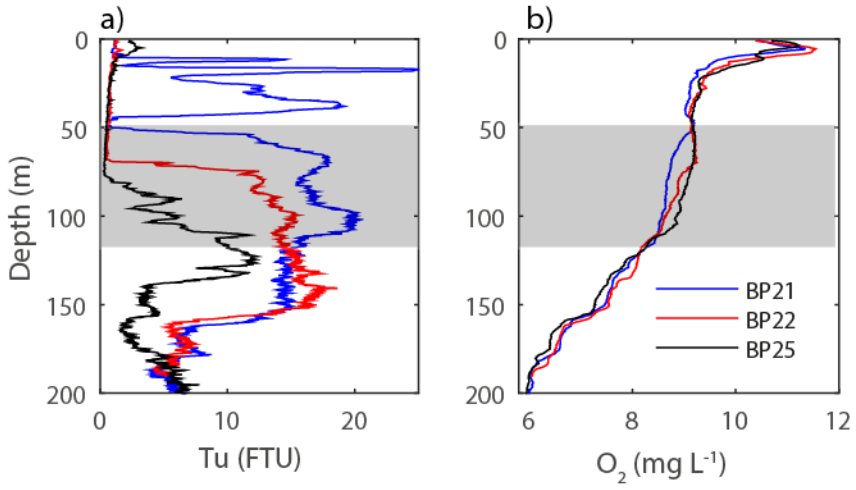

a)
b)
Depth (m)
0
50
100
150
200
0
10
20
Tu (FTU)
6
8
10
12
O_2 (mg L^{-1})
BP21
BP22
BP25

Figure 4

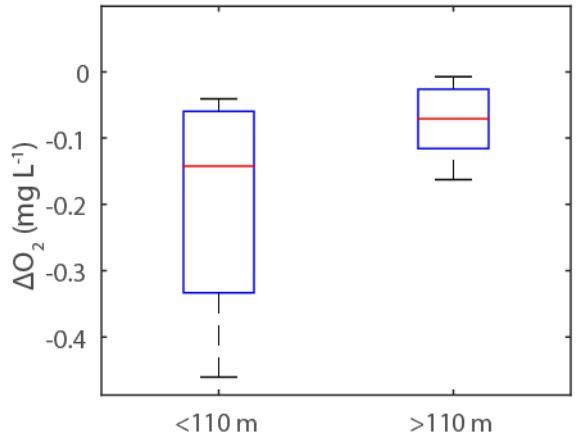


Figure 5

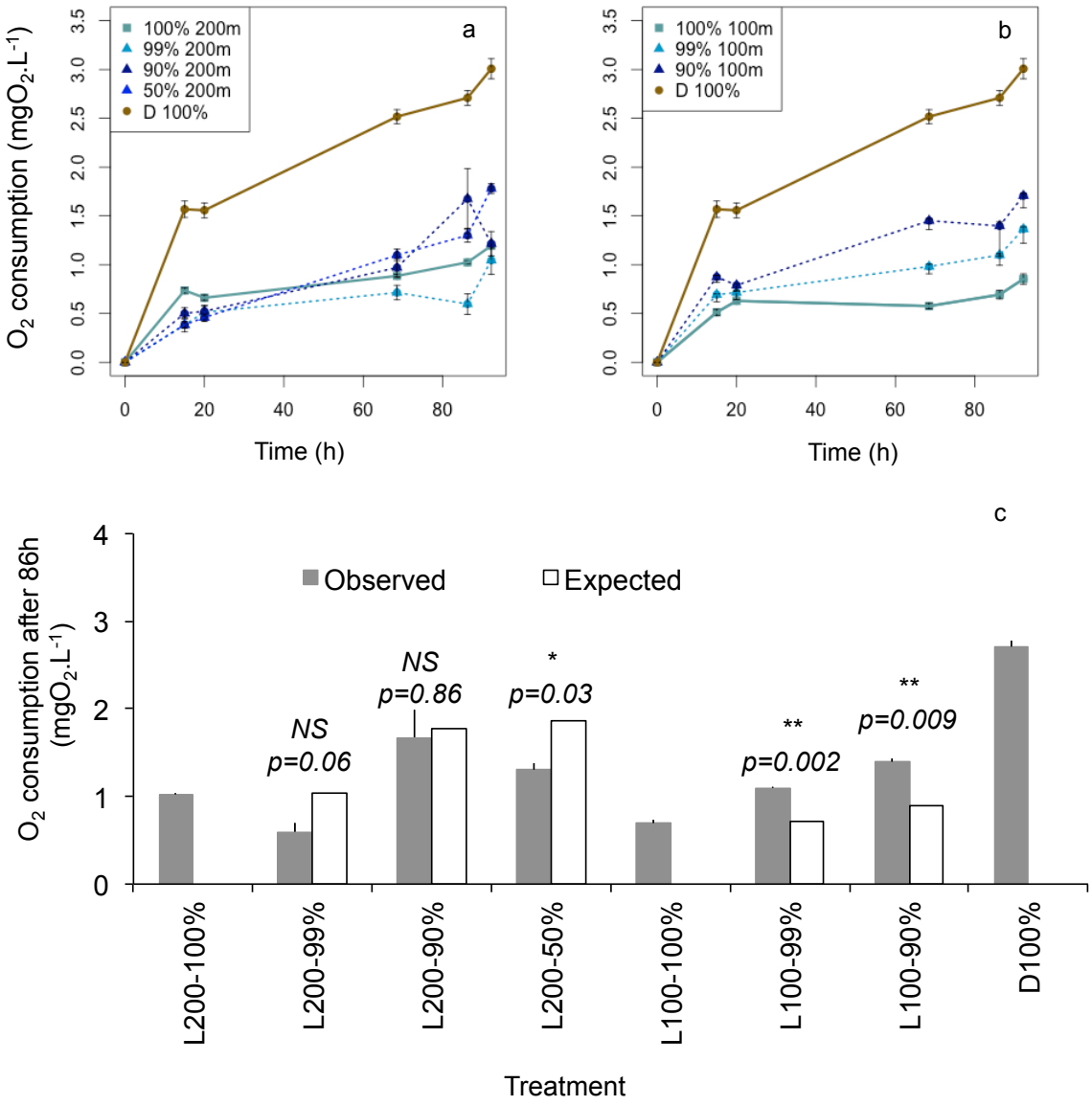

a
100% 200m
99% 200m
90% 200m
50% 200m
D 100%
O2 consumption (mgO2.L-1)
Time (h)
b
100% 100m
99% 100m
90% 100m
D 100%
Time (h)
c
Observed
Expected
O2 consumption after 86h (mgO2.L-1)
NS p=0.06
NS p=0.86
* p=0.03
** p=0.002
** p=0.009
L200-100%
L200-99%
L200-90%
L200-50%
L100-100%
L100-99%
L100-90%
D100%
Treatment

Figure 6

1

2