Physical-biological interactions controlling the variability of oxygen fluxes across the sediment-water interface

by

Erni Murniati

born in Rajagaluh, Indonesia

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Thesis examiners:

Prof. Dr. Andreas Lorke, Universität Koblenz-Landau
Dr.-Ing. Herlina, Karlsruher Institut für Technologie

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Publications

This thesis is based on the following publications (ordered by publication date):

Murniati, E., S. Geissler, and A. Lorke. (2015). Short-term and seasonal variability of oxygen fluxes at the sediment–water interface in a riverine lake. Aquatic Sciences, 77(2), 183-196. doi:10.1007/s00027-014-0362-7

Murniati, E., D. Gross, H. Herlina, K. Hancke, R. N. Glud, and A. Lorke. (2016). Oxygen imaging at the sediment-water interface using lifetime-based laser induced fluorescence (τLIF) of nano-sized particles. Limnology and Oceanography: Methods, 17(8), 506-517. doi:10.1002/lom3.10108

Murniati, E., D. Gross, H. Herlina, K. Hancke, and A. Lorke. (2017). Effects of bioirrigation on the spatial and temporal dynamics of oxygen above the sediment-water interface. *Freshwater Science, 36*(4), 784-795. doi: 10.1086/694854

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Summary

The physical-biological interactions that affect the temporal variability of benthic oxygen fluxes were investigated to gain improved understanding of the factors that control these processes. This study, for the first time is able to resolve benthic diffusive boundary layer (DBL) dynamics using the newly developed lifetime-based laser induced fluorescence (τLIF) oxygen imaging system, which enables study of the role of small-scale fluid mechanics generated by benthic organism activity, and hence a more detailed analysis of oxygen transport mechanisms across the sediment-water interface (SWI).

The net benthic oxygen flux across the sediment-water interface is controlled by sediment oxygen uptake and oxygen transport. While the oxygen transport is largely influenced by turbulence driven by large-scale flows, sediment oxygen uptake is mainly affected by oxygen production and biological- and chemical-oxygen degradation of organic matter. Both processes can be enhanced by the presence of fauna and are intimately coupled. The benthic oxygen flux can be influenced by fauna in two ways, i.e. by modulating the availability of oxygen, which enhances the sediment oxygen uptake, and by enhancing the transport of oxygen.

In-situ and a series of laboratory measurements were conducted to estimate the short- and seasonal variability of benthic fluxes including the effects of burrow ventilation activity by tube-dwelling animals using eddy correlation (EC) and τLIF oxygen imaging techniques, respectively.

The in-situ benthic oxygen fluxes showed high variability at hourly and seasonal timescales, where statistical analysis indicated that current velocity and water depth were the most significant predictors of benthic oxygen flux at the waterside, which co-varied with the discharge, temperature, and oxygen concentration. The range of variability of seasonal fluxes corresponded to the friction velocities which were driven by large-scale flows. Application of a simplified analytical model that couples the effect of hydrodynamic forcing of the diffusive boundary layer with a temperature-dependent oxygen consumption rate within the sediment showed that friction velocity and temperature cause similar variability of the steady-state benthic oxygen flux.

The application of τLIF oxygen imaging system in bioturbation experiments enabled the investigation and discovery of insights into oxygen transport mechanisms across the sediment-water interface. Distinct oxygen structures above burrow openings were revealed, these were associated with burrow ventilation. The DBL was degraded in the presence of burrow ventilation. Advective transport generated by the energetic plumes released at burrow outlets was the dominant transport driving mechanism. The contribution of diffusive flux to the total estimated decreased with increasing larval density. For a range of larvae densities, commonly observed in ponds and lakes, sediment oxygen uptake rates increased up to 2.5-fold in the presence of tube-dwelling animals, and the oxygen transport rate exceeded chironomid respiration by up to a factor of 4.

The coupled physical-biological factors affecting net benthic oxygen flux can be represented by temperature, which is a prominent factor that accounts for both oxygen transport and sediment oxygen uptake. Low oxygen transport by flow coincided with high summer temperatures, amplified by a reduction of benthic population density and pupation. It can also, however, be offset by increased ventilation activity. In contrast, low temperature coincided with high oxygen concentrations, an abundance of larvae, and higher flow is offset by less burrow ventilation activity. Investigation of the effect of hydrodynamics on oxygen transport alone suggested that the expected increase of benthic oxygen flux under global warming can be offset by a reduction in flow velocity, which could ultimately lead to increasing carbon burial rates, and in a growing importance of anaerobic mineralization pathways with increasing emission rates of methane.

This study suggests a significant contribution of biological induced benthic oxygen flux to physical transport driven by large-scale flow-fields contributing to bottom-boundary layer turbulence.

Structure of thesis

This thesis focuses on the physical-biological interactions that affect oxygen flux across the SWI. The thesis is based-on and summarizes the published articles. More specific information and detailed methods applied can be found in these corresponding articles provided in the appendices.

Chapter 1 Introduction provides background information on processes related to benthic oxygen flux across the SWI. The influence of benthic organisms on the oxygen availability and on the advective transport of oxygen induced by benthic organism activity in the sediment as well as its interactions are introduced. Available techniques to estimate oxygen flux across the SWI are presented.

Chapter 2 Objective describes the knowledge gaps, objectives, research questions and hypotheses. In **Chapter 3 Outline,** the contribution of the manuscripts to the objectives of the study is outlined. **Chapter 4 Discussions** elaborates the results of the study answering the research questions and hypotheses. **Chapter 5 Conclusion and outlook** contains the summary of the study and the recommendations for the future challenges.

References are provided at the end of Chapter 5. The published manuscripts as well as additional data/information are provided in the **appendices**.

Chapter 1
Introduction

Water covers most parts of the earth, while only tiny fractions (less than 0.01%) of the earth landscape holds freshwater lakes and rivers for various purposes (Jackson et al., 2001). Inland waters, however, play an important role in the global carbon cycle (Downing, 2010; Tranvik et al., 2009) by receiving the terrestrial organic carbon and recycling it in aquatic sediments (Cole et al., 2007). The rates of the terrestrial organic carbon delivered to inland waters as well as the carbon mineralization and burial rates within aquatic systems are globally affected by anthropogenic activities and climate change (Gudasz et al., 2010; Regnier et al., 2013; Trimmer et al., 2012).

The benthic oxygen availability in water is fundamental to sustain life in aquatic ecosystems and to regulate many important biogeochemical processes (Glud, R.N., 2008), e.g. mineralization rates in freshwater sediments (Sobek et al., 2009), oxidation of organic matters (Cai & Reimers, 1995) including biota populations (Kajak, 1997). Furthermore, the oxygen fluxes into aquatic sediments correspond closely to the reverse fluxes of carbon dioxide (CO_2) from the sediment (Granéli, 1979a), and therefore can be used as a proxy for mineralization rates (Glud, R.N. et al., 2016; Gudasz et al., 2010) to estimate global carbon budgets (Seiter et al., 2005). A process-based understanding of how oxygen is transported and the quantification of the benthic oxygen flux, which is affected by changing environmental conditions in aquatic ecosystems is therefore of utmost important for evaluating the biological status of the environment, and thus for improving the quality conditions of aquatic systems.

The benthic oxygen flux is known to vary temporally and spatially, and therefore a methodological problem sourced from the present available techniques is involved in measuring its rate. The oxygen flux across the sediment-water interface is controlled by sediment oxygen consumption/production (sediment-oxygen uptake) and transport of oxygen. While the oxygen transport is largely influenced by turbulence driven by large-scale flows (Brand, 2007; Lorke et al., 2003), the sediment oxygen consumption is mainly affected by the biological- and chemical-degradation of organic matter. Both processes can be enhanced by the presence of fauna (Moodley et al., 1998) and are intimately coupled (Boudreau & Jørgensen, 2001). Temperature plays into these influencing processes, e.g. mineralization and respiration rates (Gudasz et al., 2010) as well as benthic animals activities (Baranov et al., 2016a; Roskosch et al., 2012) including their populations (Hempel, 2010; Kajak, 1997). The local hydrodynamics and biological community under which the measurement is performed may cause the temporal variation of the oxygen fluxes, which has been observed on time scales from minutes to days (Brand et al., 2008; Bryant et al., 2010a; Lorke et al., 2012).

Two broad categories of reactions and transport processes that supply or consume solutes and particulates are present to determine factors controlling the benthic oxygen flux across the SWI. Reactions cause the production or consumption of solutes within sediments by either biologically mediated or abiotic means, while transport processes cause the spatial displacement of solutes and solids, which can also be generated by faunal activities (Gutiérrez & Jones, 2006; Mermillod-Blondin, Florian & Rosenberg, 2006). However, the interactions between physical (e.g. flow and temperature) and biological (benthic animal activity, e.g. bioturbation) factors have never been comprehensively examined.

The total benthic flux can be estimated by deploying the benthic chamber (BC) or using the eddy correlation/covariance (EC) method, while the diffusive flux can be estimated using the thin boundary layer (TBL) analysis, e.g. using microprofiler. The total benthic oxygen flux is a net integrative measure of all oxygen-consuming/producing, both chemical and biological oxygen transport processes, while the diffusive flux omits the spatial heterogeneity effects of fauna (Archer & Devol, 1992; Glud, R.N. et al., 1994). The total and the diffusive oxygen fluxes could be equal if it is met the following conditions: flat bed with insignificant topography, non-porous sediment with insignificant advective porewater flow (no-slip condition, velocity = 0 at the interface), insignificant fauna and bioirrigation, and the sediment surface and the flow does not get disturbed by the measuring technique. These conditions are rarely met in nature, such as indicated by a signification correlation between the difference of the total and diffusive oxygen flux estimates and the density of the benthic fauna (Glud, R.N. et al., 1994).

The introduction of in situ oxygen microelectrode profiler enables direct measurement of the oxygen flux between the sediment and water, which improves the understanding on the sediment biogeochemistry and oxygen flux across the sediment-water interface (Viollier et al., 2003), while introduction of the EC technique (Berg et al., 2003) as a non-invasive method helps the understanding of the spatially and temporally variability of the oxygen flux. As a more traditional method, the BC technique provides a simple application, however, it is still a subject of debate particularly on the theoretical aspect due to the artificial hydrodynamics inside the chamber, even though measurements have confirmed that no significant difference on what methods are applied (Bryant et al., 2010b; Tengberg et al., 2005).

On the three methods mentioned above (the BC, EC, and TBL methods), only the TBL method provides valuable insight on the oxygen transport mechanism across the sediment-water interface. In combination with a micro-stepper, the oxygen concentration can be profiled within 50 µm interval (Jørgensen & Des Marais, 1990). Using this method, the diffusive boundary layer (DBL) was revealed and to a large extend its thickness is regulated by the flow (Jørgensen & Revsbech, 1985) thus the turbulence level in the bottom boundary layer (Lorke et al., 2003). Both rapid and short residence time of turbulence driven variations in the DBL thickness make the DBL thickness a difficult parameter to resolve (O'Connor & Hondzo, 2008; Røy, H. et al., 2004). As an invasive method, insertion of the microsensor into the DBL can disrupt boundary layer flow, which can lead to compression of the DBL and thus its thickness (Glud, R. N. et al., 1994). Furthermore, the DBL is often difficult to analyze in the presence of the faunas that rework the sediment and ventilates their burrows. Bioturbation by benthic animals, however, is of general importance because the enhanced oxygen flux into the sediment stimulates aerobic respiration and can possibly be accompanied by enhanced exchange of solutes between sediment and overlying water (Hölker et al., 2015; Matisoff & Wang, 1998; Mermillod-Blondin, F. et al., 2004).

To resolve the required spatial and temporal variations in the DBL, imaging techniques, such as laser induced fluorescence (LIF) technique and planar optode is commonly used. These imaging techniques have become an important tool for studying processes that control the spatial and temporal variations of oxygen concentration in aquatic ecosystems, such as gas exchange at water surfaces (Herlina, H. & Jirka, 2004; Schladow et al., 2002) and around individual bubbles (Dani et al., 2007; Francois et al., 2011) as well as the flow-driven metabolic and uptake rates at sediment-water interfaces (Precht et al., 2004; Stief, P. et al., 2010) including the effects of bioturbation (Wenzhöfer & Glud, 2004) and rhizosphere dynamics (Frederiksen & Glud, 2006). However, while the LIF technique is limited to applications surrounding a bubble or at air-water interface due to the sorption of the fluorescent dye to organic surfaces, planar optode is mainly applied within the sediment, where it can be assumed that the disturbance of the flow structure caused by its sensing element does not affect the oxygen concentration distribution.

Prior to this study, no measurement technique was available to investigate the oxygen transport mechanism across the sediment-water interface in the presence of flow, the benthic organism activities and in natural organic sediments. This has impeded a more detailed analysis on the oxygen transport mechanisms across the sediment-water interface thus the controlling factors of the benthic oxygen flux, particularly in the presence of benthic organism activities. In this study, we developed an oxygen imaging system based on the lifetime-based laser induced fluorescence (τLIF) technique. The τLIF oxygen imaging system was applied to investigate the effect of fauna activity on the benthic oxygen flux including the insight on oxygen transport mechanism across the sediment-water interface.

In the following sections, processes that influence the benthic oxygen flux will be described including the available measurement techniques.

1.1 Sediment oxygen consumption

Oxygen is used for aerobic respiration of organism which directly oxidize organic matter or it is used to microbially or chemically reduced products (i.e. NH_4^+, Fe^{2+}, Mn^{2+}, H_2S and CH_4). Below are oxygen-consuming processes in nutrient cycles, i.e. processes that require oxygen, e.g. aerobic respiration, nitrification and chemical oxidation or reduced substances.

Aerobic respiration

Oxygen is an important determinant for stability/quality of life and survival of living organisms. All plants and animals require oxygen for respiration (aerobic respiration). During low oxygen concentration that fall below 2 mg L^{-1}, the water is considered hypoxic. Under anoxic condition (zero oxygen concentration), bacteria decompose organic matter, generate energy by the oxidation of nutrients and use an external electron acceptor other than oxygen, such as sulfate (SO_4^{2-}) and nitrate (NO_3^-).

Nitrification and chemical oxidation of reduced substances

Nitrification requires oxygen as electron acceptor by the support of microbes in a two-step process which is performed by a different group of bacteria: 1) First step: oxidation of ammonia (NH_3) to nitrite (NO_2^-) brought by ammonia oxidizing bacteria (e.g. *Nitrosomonas*, *Nitrosococcus*, *Nitrosolobus*) and 2) Second step: nitrite (NO_2^-) produced from the first step is oxidized to nitrate (NO_3^-) by the support of nitrite (NO_2^-) oxidizing bacteria (e.g. *Nitrococcus*, *Nitrobacter*, *Nitrospira*, *Nitrospina*).

Most of the reduced substances in the sediments, i.e. iron (Fe^{2+}), manganese (Mn^{2+}), hydrogen sulfide (H_2S) and methane (CH_4) are products of the microbially-mediated anaerobic decomposition from organic material. The production of these reduced substances is built up during low bottom oxygen concentration.

Excess availability of nutrients stimulates not only primary production, but also has significant effects on microbial processes which lead to oxygen depletion. When the oxygen concentration is depleted, the nitrification pathway is stopped which may lower the release of nitrogen gas and retain the nutrient in bio-available forms (NH_4^+, $H_2PO_4^-$ or HPO_4^-). As a consequence, hydrogen sulfide (H_2S) may accumulate and the sediments tend to release iron and phosphorus into the water column, which may fuel algal grow and sustain a continuous supply organic matter into the sediment.

The oxygen consumption by the sediment is therefore linked closely to the presence of microbial or fauna community, which depends on the availability of organic matters and oxygen concentration in the overlying water, which in turn affects the water quality conditions, especially oxygen concentration in the overlying water. While a large number of literature has been dealing with the sediment oxygen consumption with its related processes (e.g., in Bianucci et al. (2012), Ford et al. (2002) and Moodley et al. (1998)), this closed relationship has been described in a changing environment, particularly due to changing nutrient loadings and rising temperatures (Meire et al., 2013) and its consequences to ecosystem functioning (Villnas et al., 2012).

1.2 Benthic oxygen flux

The region in the vicinity of the sediment-water interface represents most complex and unpredictable interactions between organisms and their physical-chemical environments (Fig. 1.1). In this zone, most of the processes take place: 1) physical forcing, e.g., dampening of current, wave and turbulent energies, 2) biological activities, e.g., burrow ventilation and bioirrigation, and 3) abiotic structures, e.g. sediment deposition and re-suspension, sediment roughness, and sediment topography. The oxygen in water is transported by advective transport and/or by concentration gradient through diffusion. Among physical variables, flow is the most significant factor affecting the solute transport across the sediment-water interface (SWI). The components which involve in the benthic oxygen flux processes will be described in the following sections.

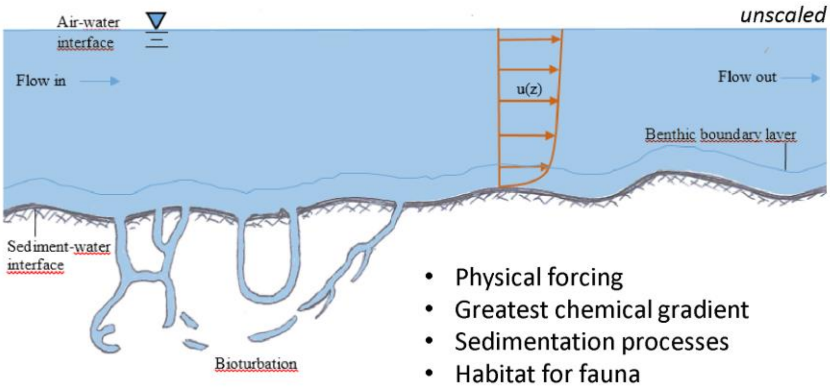

Fig. 1. 1: Illustration of dynamic and complex interactions of the physical-biological functions related to the oxygen flux across the sediment-water interface. source: modified from Santschi et al. (1990) and Socolofsky and Jirka (2004).

Benthic boundary layer

The vertical region above the bottom sediment is termed the benthic boundary layer (BBL). Based on the physical properties, the elements of the BBL ideally comprise the diffusive boundary layer (DBL), the viscous sub-layer, the logarithmic layer, and the Eckman layer (Aller et al., 2001). Within the water column near the sediment-water interface, strong gradient in physical-chemical properties, such as oxygen is developed due to the physical forcing and the presence of the sediment-water interface (SWI). The flow velocity is changed from being turbulent in free stream region to laminar near the SWI, while oxygen is taken up by the sediment within a sediment layer in mm scale (Fig. 1.2).

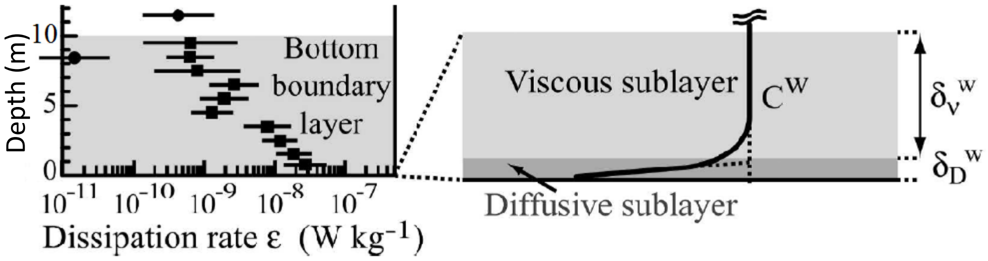

Fig. 1. 2: Linking the hydrodynamic forcing in the bottom boundary layer represented by turbulence dissipation rate ε (left panel) and oxygen concentration profile (right panel) within diffusive boundary layer. source: modified after Lorke and Peeters (2006).

The thickness of the BBL is defined by the height of frictional velocity. Within centimeter scale, the internal friction induced by water flow starts to compete against the viscosity creates the viscous sub-layer over the sediment surface. Closer to the interface, a film of water tends to stick to the solid surface and does not follow the general circulation of the water created the diffusive boundary layer (DBL).

For running waters, eroded sediment makes the interpretation of the sediment-water interface difficult. Only in the zone with moderate flow velocity that does not cause resuspension of the sediment, this layer can be clearly defined. Adding to the complexity, the combination of the water flow and sediment surface topography may induce lateral pressure gradients that drive advective flow near the interface. In addition, the surface roughness of the sediment affects the friction velocity of the overlying flow, and thus the thickness and geometry of the diffusive boundary layer. Additional source of advective flow near the interface can also be caused by benthic organism.

Physical forcing

The mass transfer is a summation of flow transport process (advective flux) and molecular transport processes (diffusive flux). Advection is a transport process that is due to the motion of the fluid, while diffusion is due to the mean concentration gradient over time. The advection-diffusion equation along x-axis is:

$$\frac{\partial C}{\partial t}+u\frac{\partial C}{\partial x}=D\frac{\partial^2 C}{\partial x^2} \quad or \quad \frac{\partial C}{\partial t}=\frac{\partial C}{\partial x}\cdot\left(D\frac{\partial C}{\partial x}-u\right) \qquad 1.1$$

The instantaneous velocity u and concentration C comprise the mean and fluctuation components (Reynolds-decomposition):

$$u=\bar{u}+u'; \quad C=\bar{C}+C' \qquad 1.2$$

Temporal averaging of the 1D advection-diffusion equation is:

$$\frac{\partial \bar{C}}{\partial t}+\bar{u}\frac{\partial \bar{C}}{\partial x}+\frac{\partial}{\partial x}\overline{u'C'}=D\frac{\partial^2 \bar{C}}{\partial x^2} \quad or \quad \frac{\partial \bar{C}}{\partial t}+\bar{u}\frac{\partial \bar{C}}{\partial x}=\frac{\partial}{\partial x}\cdot\left(D\frac{\partial \bar{C}}{\partial x}-\overline{u'C'}\right) \qquad 1.3$$

which represents the physical transport of concentration by advection $\bar{u}\frac{\partial \bar{C}}{\partial x}$, by molecular diffusion $D\frac{\partial^2 \bar{C}}{\partial x^2}$, and by turbulent diffusion $\frac{\partial}{\partial x}\overline{u'C'}$. The $\overline{u'C'}$ is the correlation between the velocity and concentration fluctuation components.

Thus, the flux governed by molecular diffusion is:

$$F_{x,mdif}=-D\frac{\partial \bar{C}}{\partial x} \qquad 1.4$$

and the flux governed by turbulent diffusion is:

$$F_{x,turb}=\overline{u'C'} \qquad 1.5$$

The turbulent advection is the dominant vertical transport in the water column where the flow velocity is decreasing from being turbulent in the free-stream region to being laminar near the SWI and no concentration gradients exist. Therefore, in the free-stream region when no mean temporal concentration gradients are present, the oxygen flux can be assumed to be exclusively coming from turbulent motions. Near the interface, the turbulent dies out and the molecular diffusion becomes the principal mechanism for mass transport across the SWI. At steady state condition, i.e. $\frac{\partial C}{\partial t} = 0$, the vertical oxygen concentration ($C = f(z)$) is:

$$\frac{\partial^2 C}{\partial z^2} = 0 \qquad 1.6$$

with boundary conditions: C_0 at $z = 0$ and C_∞ at $z = \delta_{DBL}$, the oxygen concentration C at any given depth z is:

$$C(z) = \frac{C_\infty - C_0}{\delta_{DBL}} \cdot z + C_0 \qquad 1.7$$

Thus, the diffusive flux F_{DBL} becomes:

$$F_{DBL} = -D \cdot \frac{C_\infty - C_0}{\delta_{DBL}} \qquad 1.8$$

where the δ_{DBL} is the thickness of the diffusive boundary layer. The oxygen flux therefore can be described as a product of a gas transfer velocity k and the oxygen concentration gradient across the SWI:

$$F_{DBL} = k(C_\infty - C_0) \qquad 1.9$$

where $k = \frac{D}{\delta_{DBL}}$.

Turbulence generation. In aquatic systems, turbulence can be generated by wind-shear, bottom-shear (current), and density gradient (e.g., due to temperature or salinity), or combinations of those factors. While the turbulence in the water that affecting solute exchange across the air-water interface is predominantly generated by wind-shear, the turbulence near to the sediment-water interface can be originated from, e.g. bottom-shear induced turbulence in rivers or lotic systems or from buoyant convection due to temperature gradient in littoral regions or sloping boundaries (Lorke et al., 2008). In addition, aquatic sediment is a habitat for many infauna or insects during larva stage. Activities of these organisms can also create flow (Munksby et al., 2002; Roskosch et al., 2010).

The flow can be laminar or turbulent, though most of the flows in nature are turbulent. The turbulent flow is mostly represented by Reynolds numbers which is defined by the ratio of inertia force and friction force:

$$Re = \frac{\rho \bar{u} l}{\eta} \qquad 1.10$$

where ρ is density, $\bar{u}$ is mean velocity, l is characteristic length scale and η is dynamic viscosity.

The physical properties of the aquatic environment of the transport process ranges over the vast spectrum of scales (Fig. 1.3). Benthic organisms live in a low Reynolds numbers dominated by viscous forces. However, they are important for the nutrient uptake and for the transfer of dissolved substances across the sediment-water interface.

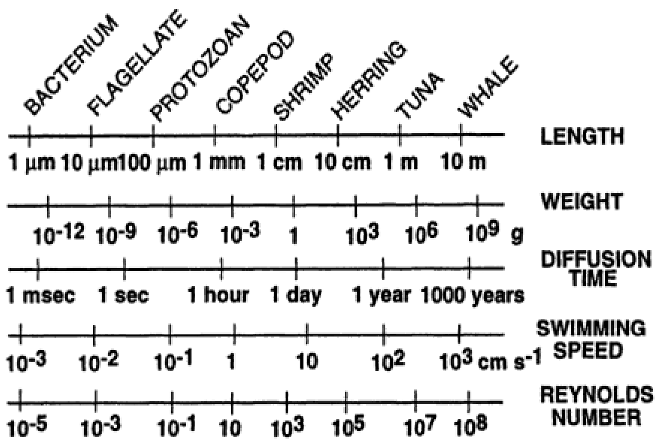

Fig. 1. 3: Spectrum of the transport scale of biological and physical properties. source: Aller et al. (2001)

Solute transport across the SWI

As mentioned before, the benthic oxygen flux can be attributed to sediment oxygen uptake (the net exchange between production and consumption, and its transporting processes. The reactions and transport processes are closely coupled (Boudreau & Jørgensen, 2001). For example, Cai and Sayles (1996) described the relationship between transport of oxygen to the sediment and the penetration depth of oxygen in the sediment, which depends on oxygen consumption in the sediment and the oxygen availability in overlying water (Cai & Reimers, 1995; McGinnis et al., 2014). Oxygen penetration depth has been considered as critical parameter that influences the fate of oxidation of reduced substances, which is one of oxygen consuming factors.

Quantification of the benthic oxygen flux can be assessed from either the sediment- or water-sides. The transport of oxygen through the water side of the BBL must cross the DBL and the benthic oxygen exchange rate (i.e., the flux) may depend on the rate of transport across this DBL. A most simple case is the diffusive flux across a solid, impermeable structure that is exposed directly to the boundary layer flow with no-slip condition with reactions that takes place directly on its surface. Within the DBL, the time-average concentration gradient is linear (Boudreau, 2001). Based on the simple film theory for mass transfer across a diffusive boundary layer using Fick’s Law, the benthic oxygen flux can be estimated (Eq. 1.8).

The benthic oxygen flux assessed from the sediment-side can be modeled using zero-order consumption as presented in Fig. 1.4 (Boudreau & Jørgensen, 2001):

$$F_{sed} = -\frac{\varphi D}{\theta^2}\frac{dC}{dz}\bigg|_{z=0} \qquad 1.\,11$$

where D is the molecular diffusion coefficient for the solute, φ and θ are the porosity and tortuosity of the sediment, respectively, and dC/dz in the concentration gradient at the SWI in the sediment-side. A good agreement has been obtained by applying this zero-order consumption model to the oxygen profile, both on the water- and sediment sides.

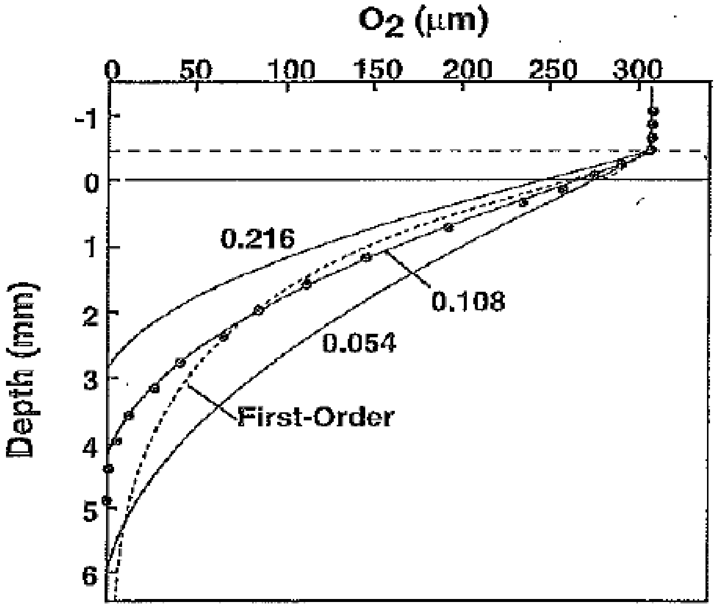

Fig. 1. 4: Zero-order kinetic model fitting the oxygen profile in the BBL from both sediment- and water sides as described by Eq. 1.23 (Boudreau & Jørgensen, 2001).

The benthic oxygen transport is largely influenced by turbulence driven by large-scale flows, such as internal seiche (Brand et al., 2008; Bryant et al., 2010a; Lorke et al., 2003), bottom-shear and convective mixing in sloping boundary (Lorrai et al., 2011) as well as faunal activities (Wenzhöfer & Glud, 2004), while the benthic oxygen uptake is mainly controlled by the availability of oxygen concentration in the overlying water, organic matter available for decomposition, sediment resuspension, photosynthetic and benthic organism activities, salinity, pH, chemical oxygen demand as well as temperature (Bowman & Delfino, 1979).

1.3 Faunal influences on benthic oxygen flux

Bottom sediment is not only the site where the gradients in physical, chemical, and biological properties at the greatest indicating most biogeochemical processes occurred in the vicinity of the sediment-water interface, but also serves as habitat for benthic organisms. Sediments are inhabited by abundant and diverse populations of fauna (Wallace & Anderson, 1996). Sediments are also the place where organic matter settled in which some are mineralized and the released nutrients are transported to the overlying water (Nunnally et al., 2013).

The tube-dwelling animals, such as *Chironomus plumosus* can influence the oxygen fluxes via two ways, i.e. by enhancing the sediment oxygen consumption and by generating flow through burrow ventilation. Burrow ventilation by tube-dwelling benthic animals introduces oxygen-rich water into the burrow thus increasing the oxygen availability, which is then diffused into surrounding sediment, and termed as bioirrigation (Fig. 1.5). During their activities they also change the sediment topography and alter the sediment stratification and its porosity by means of particle reworking. A combined activity of burrow ventilation and particle reworking is defined as bioturbation (Kristensen et al., 2012).

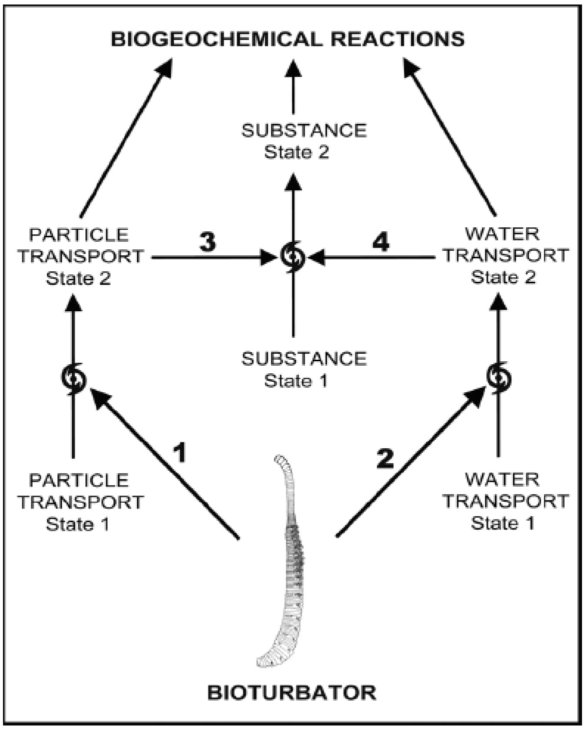

Fig. 1. 5: Ecosystem engineering by bioturbating animals (bioturbators) that affects biogeochemical conditions in sediment is a combined process of particle transport (sediment movement) and water burrow ventilation (water movement). Process 1: particle transport (i.e. reworking), which is driven by burrowing and deposit feeding. By means of biomixing, Process 1 can lead to Process 3, which modifies the sediment chemically, e.g. modified substance (e.g. faeces). Burrow ventilation by the bioturbator transports water in and out of burrows (Process 2). By introducing oxygen and removing of toxic metabolites, bioirrigation (Process 4) may modify the chemical (e.g. redox) state of pore water (substance) surrounding burrows (Process 4). It might also occur that bioturbation affect only to transport processes, i.e. redistribution of particles and water, without changing chemical states. source: Kristensen et al. (2012).

Sediment oxygen uptake

The sediment oxygen uptake is an integrative measure of all oxygen-consuming/producing processes, both chemical and biological (Hargrave, 1972b). Oxygen in overlying water may be consumed primarily by bacterial, although algae, protozoa, and fungi may also contribute. Reducing substances are usually rapidly oxidized. Whatever populations are involved, measurements of sediment oxygen uptake reflect the metabolism of communities of microorganisms involved in the decomposition of natural substrates.

The enhancement of sediment oxygen uptake promoted by benthic animals has been examined in numerous studies (Baranov et al., 2016b; Hansen et al., 1998; Hargrave, 1972a; Matisoff & Wang, 1998; Pelegri & Blackburn, 1996). Specific to *C. plumosus*, bioirrigation can enhanced sediment respiration by a factor of 2-4 (Baranov et al., 2016b; Granéli, 1979c; Svensson & Leonardson, 1996).

The sediment oxygen uptake enhancement by benthic animals has been observed to depend on species (Brodersen et al., 2008; Matisoff & Wang, 1998), on larval stage (Adamek & Fischer, 1985), and its abundance as well as on overlying oxygen concentration and temperature (Baranov et al., 2016a; Roskosch et al., 2012). The abundance of the benthic animal in the sediment may also depend on several factors, such as sediment temperatures (Hilsenhoff, 1966), overlying oxygen concentration (Kajak, 1997) and the availability of organic materials (Pinder, 1986). Its abundance can be varied seasonally (Hempel, 2010; Maténa, 1989).

Bioturbation

As depicted in Fig. 1.5, bioturbation is disturbances caused by organisms (bioturbators), particularly in aquatic sediment, e.g. in/on river/lake-bed or ocean's floor which changes the physical properties of sediment and/or solute concentration. Bioturbation can be caused by a variety of benthos, i.e. epifauna (organism living on the sediment surface) or infauna (organism living inside the sediment), which can be insects during larval stage as well as macro invertebrates and benthivorous fish. Kristensen et al. (2012) categorized bioturbation into burrow ventilation (water movement) and particle reworking (sediment movement). Burrow ventilation is the activity of the organism which transport water hence dissolve solute contained in the water, while particle reworking is defined as the results of the activities of organisms that deform the sediment surface topography as well as its structure (porosity) and texture (sediment stratification).

Burrow ventilation. Some of the benthic animals construct a burrow and circulate oxic water for their filter feeding. The burrow may have an open-end (J-shaped) or closed-end (U-shaped) tube (Riisgård & Larsen, 2005). These tube-dwelling animals, such as *C. plumosus* circulate the water through the tube, i.e. the overlying water is drawn to the tube from the inlet and released through an outlet for respiration and filter feeding. Burrow ventilation is generated by undulations of their approximately 20 mm long body, which travels in the head-to-tail direction as sinusoidal wave (Brackenbury, 2000). In the burrow they trap particles/planktons for feeding purposes by constructing a conical net (Walshe, 1947). In alternating periods of pumping and resting, the larvae draw oxygen-rich water into the burrow, absorb and store the oxygen in hemoglobin, while during the periods of feeding or resting the oxygen in the hemoglobin is used for metabolism (Walshe, 1950). The movement of larva in the tube creates three-dimensional flow fields above the burrow inlet and outlet (Morad et al., 2010; Munksby et al., 2002; Roskosch et al., 2010) as well as complex three-dimensional concentration distribution in the sediment (Lewandowski & Hupfer, 2005). The enhanced benthic oxygen fluxes stimulate aerobic respiration and are accompanied by enhanced exchange of solutes between sediment and overlying water (Hölker et al., 2015; Matisoff & Wang, 1998; Mermillod-Blondin, F. et al., 2004).

Sediment reworking. The sediment surfaces are not generally smooth. The tube-dwelling animals are not only responsible for modifying the solute transport, but also can alter the sediment properties, such texture and surface roughness. Irregular microtopography of the sediment surface, for example, can influence roughness length, friction velocity of the overlying water, and thus the benthic oxygen flux (Røy, Hans et al., 2002). For some benthic animals, such as *Pysgospio elegans, C. riparius, and C. dorsalis*, the inlet of the tube is typically observed to extend a few millimeters above the surrounding sediment assuming to bypass the low oxygen concentration region of the boundary layer overlaying a sediment-water interface (SWI) (Jørgensen & Revsbech, 1985; Pinder, 1986; Stief, Peter et al., 2005).

1.4 Techniques for measuring oxygen flux across the SWI

A short-list of methods to measure the oxygen flux in the benthic boundary layer is available, i.e. the benthic chamber (BC) and the thin boundary layer (TBL) analysis. During the last decade, the eddy correlation (covariance) method was introduced to estimate the benthic oxygen flux facilitated by the availability of fast response velocity and concentration sensors (Berg et al., 2003). The methods have their pros and cons, while the application depends on the suitability and its assumptions.

Benthic chamber (BC) method

The oxygen flux across the SWI is measured by deploying a chamber to a designated location isolating a limited area of the sediment surface including the overlying water. The oxygen flux is then calculated from concentration change over time. The oxygen concentration change is measured either in-situ with sensors or by extracting water from inside the chamber and analyze the discrete water sample later.

The flux (F) is calculated from a linear regression of concentration over time (Aller et al., 2001):

$$F = \frac{mV_c}{A_c} \qquad 1.\,12$$

where $m = \Delta C/\Delta t$ is the slope of the linear regression, which is the concentration C increase or decrease over time (t), V_c is the volume of water in the chamber and A_c is the area of the sediment surface enclosed by the chamber.

The BC method estimates the total oxygen flux and as it is a simple method it has been applied in numerous studies (Viollier et al., 2003 and references therein). Its design and application have been improved throughout the years (Tengberg et al., 1995). The flux calculation is based on the assumptions: 1) steady state conditions during measurement, i.e. no temporal changes in the concentration gradients within sediment and between the sediment and the overlying water, 2) the rates of biogeochemical processes in overlying water column are insignificant compared to those within the sediment, 3) the hydrodynamic regime inside the chamber does not alter solute exchange compared to that of outside the chamber, 4) the sampling area where the chamber is deployed is representative for a larger area. Under in situ conditions, it may be possible that either one or more of these assumptions may not be valid, particularly due to artificial stirring, which change the hydrodynamic condition inside the chamber. The altered flow inside the chamber violates the theory of mass transport in which the flux is regulated by the flow (Jørgensen & Des Marais, 1990). However, investigations of various chamber designs and hydrodynamic conditions inside the chamber as well as different methods of comparison indicates that there is no statistical significant correlation between chamber design and hydrodynamics inside chamber with the measured fluxes (Tengberg et al., 2005) and no significant difference on what methods are to be applied (Bryant et al., 2010b).

Thin boundary layer (TBL) analysis

The oxygen flux is calculated using the measured vertical oxygen profile based on the mass-transport phenomena near the SWI either from the water- or sediment-sides. From the sediment-side, as described in Section 1.2, the oxygen flux can be model using zero-order consumption (Eq.1.11). The technique measures the vertical oxygen concentration profile within the sediment, where it can be assumed that the oxygen distribution is not affected by the flow. After the thin boundary layer of solute gradient near the SWI at the water-side is revealed (Jørgensen & Revsbech, 1985), the benthic oxygen flux estimate is extended to the water-side and determined using Eq.1.8.

The oxygen microprofiler has been deployed in situ for measuring the diffusive flux to gain insight of the biogeochemical processes of carbon and oxygen within marine environments (Viollier et al., 2003 and references therein). In the DBL and in millimeter just below the sediment, the solute exchange is mainly governed by diffusion (no net advection and no reactions). Thus the diffusive flux estimates from the TBL analysis omits the spatial heterogeneity effects of fauna (Archer & Devol, 1992; Glud, R.N. et al., 1994). Based on experimental study as well as predicted by the theory, the time-averaged concentration gradients in the DBL and just below the sediment are linear (Aller et al., 2001).

The DBL thickness is in the order of sub mm, while the oxygen penetration depth in the sediment may be in cm scale, which depends on the type of sediment (permeable or impermeable) and seasons (Boudreau & Jørgensen, 2001). To obtain the vertical oxygen concentration profile across the sediment-water interface in sub mm scale, the oxygen sensor is inserted to the sediment by means of a micro-stepper. The sediment-water interface may be detected by slightly vibrating the sensor, where the surface was then defined when surface particles started to vibrate as well (Jørgensen & Revsbech, 1985) or by identification of the break in the oxygen gradient between the sediment- and water-sides (Boudreau & Jørgensen, 2001).

Eddy correlation technique

The eddy correlation/covariance (EC) technique utilizes the turbulent eddies which transports oxygen in the water column. It relies on simultaneous measurements of vertical velocity and oxygen concentration. The EC technique adopts the flux measurement technique to measure the carbondioxide (CO_2), moisture, and energy exchange in the atmospheric boundary layer (Berg et al., 2003). The EC technique is fostered by the availability of fast-response oxygen sensor. The flux assumes that the oxygen is solely transported by turbulent eddies in the water column, which gives the oxygen flux averaged over time as described in Eq. 1.13 in vertical direction as:

$$\bar{F} = \overline{w'C'} \qquad 1.13$$

where w' and C' are the fluctuating components of the vertical flow velocity and concentration, respectively, and the overbar denotes temporal averaging. The fluctuation components are obtained by subtracting the mean values from the measured instantaneous values of vertical velocity $w(t)$ and concentration $C(t)$ based on Reynolds decomposition:

$$w(t) = \overline{w} + w'(t) \qquad 1.14$$

$$C(t) = \bar{C} + C'(t) \qquad 1.15$$

Processing the EC data is dependent on the specific hydrodynamic conditions under which the measurement is performed. Generally, it includes velocity data corrections, coordinate rotation and selection of an averaging time scale for separating the mean and fluctuating components and flux averaging time scale (Lorke et al., 2013; Lorrai et al., 2010; McGinnis et al., 2008).

The EC technique has been applied to measure the benthic oxygen flux under various hydrodynamic forcing conditions (Berg et al., 2013; Brand et al., 2008; Lorke et al., 2012) and within specific habitats (Glud, R. N. et al., 2010; Hume et al., 2011; Long et al., 2011). In contrast to the BC method, the EC technique measures the total oxygen flux without disturbing the natural hydrodynamic conditions with the contribution area to the flux is relatively larger compared to the chamber dimension (Berg et al., 2007).

Imaging technique

A high-spatial and -temporal resolutions imaging technique, such as planar optode (Santner et al., 2015) and laser induced fluorescence (LIF) technique (Crimaldi, 2008) becomes an important tool to investigate the insight of the transport and biogeochemical processes regulating the oxygen distribution and dynamics. Both methods are relied on oxygen quenching of an oxygen indicator, i.e. the lifetime or the intensity of the indicator is proportionally reduced in the presence of oxygen (Vaughan & Weber, 1970).

Compared to planar optode, which has temporal resolution of a few seconds (Polerecky et al., 2006) and spatial resolution <0.1 mm , the LIF technique can achieve temporal resolution of 8 Hz (Herlina & Jirka, 2007) with similar spatial resolution. Moreover, planar optode is not inclusively a non-invasive technique. It typically attached to a transparent sidewall of the experimental tank to observe the DO concentration distribution in the vicinity of the foil, thus the applications mostly conducted within the sediment, where the disturbance of the flow structure does not affect the oxygen concentration distribution. On the other hand, the LIF technique for oxygen imaging in flowing water are mostly based on luminescence intensity measurements of a dissolved indicator. A major limitation for applying the technique in the BBL is the sorption of the luminescent dye to organic surfaces at the sediment.

Planar optode has been mainly applied to study the flow-driven metabolic and uptake rates (Precht et al., 2004; Stief, P. et al., 2010), the effect of bioturbation (Volkenborn et al., 2007; Wenzhöfer & Glud, 2004) and rhizosphere dynamics (Frederiksen & Glud, 2006), while the LIF technique mainly has been applied to study processes across the air-water interface (Herlina, H. & Jirka, 2004; Schladow et al., 2002) or around individual bubble (Dani et al., 2007; Francois et al., 2011).

Chapter 2
Objectives

The general objective of this thesis is aimed at understanding the physical-biological interactions that affect the oxygen flux across the sediment-water interface (SWI). As described in previous chapter (Chapter 1 Introduction), we identified the following knowledge gaps:

- The net benthic oxygen flux across the sediment-water interface is controlled by sediment oxygen consumption/production (sediment-oxygen uptake) and oxygen transport. While the oxygen transport is largely influenced by turbulence driven by large-scale flows, the sediment oxygen consumption is mainly affected by biological- and chemical-degradation of organic matter. Both processes can be enhanced by the presence of fauna and are intimately coupled. The interactions between physical (e.g. flow and temperature) and biological (benthic animal activity, e.g. bioturbation) factors have never been comprehensively examined.
- As mentioned in above point, near-bed flow velocity and temperature are among previously mentioned influential physical factors that control the oxygen flux across the sediment-water interface. While flow is a predominantly controlling factor for the oxygen transport, temperature couples both oxygen transport and consumption processes. The coupled effects of temperature on the net benthic oxygen fluxes compared to the flow on oxygen transport alone have never been mutually examined.
- To date, the role of small-scale fluid mechanics, particularly the effect of benthic organism activities on the oxygen distribution above the sediment surface has not been analyzed quantitatively, which has impeded a more detailed analysis on the mechanisms of oxygen transport across the sediment-water interface, particularly in the presence of benthic organisms activity.
- The above point is partly due to the existing methodological limitation. The oxygen concentration distribution dynamics due to the benthic animal activities have mainly been studied inside the sediments. The flow field observations using particle image velocimetry (PIV) however have revealed the existence of large-scale plumes, particularly at the burrow outlets. The effect of these flows on the oxygen concentration distribution and mean vertical concentration gradients have not been investigated either.

The specific goals of this study are:

- To investigate short- and seasonal-term of oxygen fluxes across the sediment-water interface and the controlling factors that affect its variability including the effect of benthic organism activity
- To examine faunal influences on the oxygen transport mechanism across the sediment-water interface by quantifying the diffusive boundary layer (DBL) dynamics using a non-intrusive lifetime-based laser induced fluorescence technique.
- To analyze instantaneous and mean oxygen concentration distribution as well as its gradients above the sediment-water interface as a function of organism density and in relation to their ventilation activity
- To develop a suitable oxygen imaging system for doing the above points.

The study is aimed to investigate the following research questions and hypotheses:

- How and at what temporal scale does the variation in physical factors, e.g. flow and temperature affect the temporal variation of the benthic oxygen flux?

  Hypothesis 1 (**H1**): the benthic oxygen flux is governed by turbulence driven by large-scale flows.

  H2: the benthic oxygen flux varies hourly as well as seasonally.

  H3: temperature and friction velocity cause similar variability of the steady-state benthic oxygen flux.
- How can the benthic community, particularly tube-dwelling animals, such as *Chironomus plumosus* contribute to the temporal variation of the benthic oxygen flux?

  H4: The sediment oxygen consumption is enhanced by the presence of benthic organisms.

  H5: The benthic organism activity, i.e. burrow ventilation increases the oxygen transport rate.
- How does burrow ventilation affect the oxygen transport mechanism?

  H6: The flow which is generated by burrow ventilation affects the oxygen concentration distribution above the burrows.

  H7: The mean oxygen concentration gradient in the DBL is degraded.
- How does pumping activity affect the DBL thickness?

  H8: The DBL thickness is getting thinner with increasing organism density.
- How do the temporal scale variations of the physical factors (i.e. flow and temperature) and biological factors (benthic community abundance and pumping activity) affect the benthic oxygen flux?

  H9: Seasonal variations of the biological factors affect the benthic oxygen flux differently from that of the physical factors.
- How suitable does the newly developed τLIF system to quantify the DBL dynamics in the presence of flow, organism activity and natural organic sediments?

  H10: The τLIF system is able to resolve the DBL dynamics in the presence of flow, organism activity and natural organic sediments.

Chapter 3
Outline

To fulfill the objectives of the study mentioned in the previous chapter, measurements of the oxygen concentration dynamics across the sediment-water interface were conducted in in situ and laboratory measurements. The data were used to investigate the controlling factors of oxygen flux across the sediment-water interface due to the physical-biological interactions. Field measurements were conducted in a riverine lake (Fig. 3.1). To investigate the effects of the faunal activity on the oxygen dynamics above the sediment-water interface, a new measurement technique was required and has been developed (Fig. 3.2). This newly developed lifetime-based laser induced fluorescence system was applied in a series of laboratory measurements for studying bioturbation (Fig. 3.3).

In-situ measurements using eddy correlation (EC) technique in Havel River (Fig. 3.1) have been conducted to analyze various physical factors controlling benthic oxygen in riverine lakes, which covered a short- and seasonal-timescales of the benthic oxygen flux (Murniati et al., 2015). The combined effects of hydrodynamic forcing and seasonal changes in temperature on sediment oxygen uptake rate has been evaluated in detail to analyze to what extent the temperature-dependence of sediment oxygen uptake rate can be observed in in-situ flux measurements under varying hydrodynamic forcing conditions.

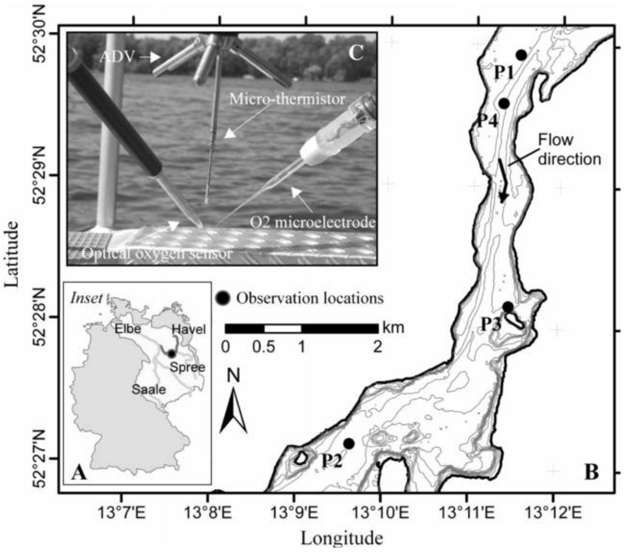

Fig. 3.1: Study site of in situ measurement using eddy correlation (EC) technique in Havel River. A) Location of the Havel River (dark grey line) within the German part of the Elbe River Basin (light grey). The location of the study area is marked by the black dot. B) Detailed map of the study area within a riverine lake section of the Havel River. The locations of the four sampling sites (P1–P4) are indicated. Grey lines show depth contours with 1 m increments. The black line is the 0 m contour. The general flow direction of the river is north to south as indicated by the arrow. C) The EC sensor arrangement included the ADV, oxygen microelectrode, optical oxygen sensor, and micro-thermistor.

We developed a new oxygen imaging system based on lifetime-based laser induced fluorescence (τLIF) technique (Fig. 3.2) (Murniati et al., 2016). The τLIF system allows for the unrestricted observation of the spatial and temporal dynamics of oxygen concentration above the sediment surface under the presence of flow, natural organic sediments, and faunal activity. Using its unique and novel features, sediment surface topography and the dynamics of oxygen concentration gradients in the top few millimeters above the sediment surface can be quantified.

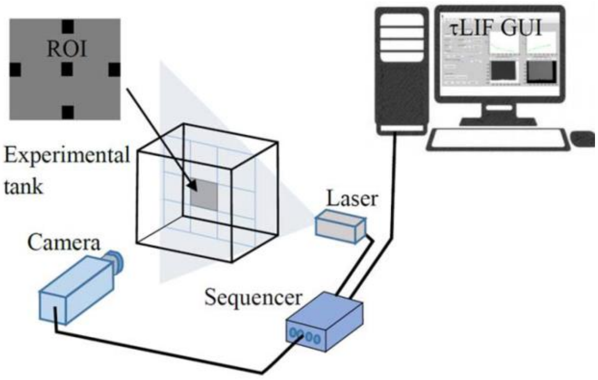

Fig. 3.2: The τLIF system consists of a laser and a camera, which are controlled by a sequencer. The light blue triangle shows the laser light sheet, which is illuminating the experimental tank from the side. The camera is positioned perpendicular to the light sheet and records image intensities within the region of interest (ROI, light gray area within the experimental tank).

A series of laboratory measurements has been conducted to evaluate the effect of faunal activity in sediment on the spatial and temporal oxygen dynamics above the sediment-water interface (Fig. 3.3) (Murniati et al., 2017). Bioturbator, such as *C. plumosus* is known to affect the solute exchange by two means, i.e. by generating flow (burrow ventilation) and increasing oxygen availability in the sediment (bioirrigation). The temporal dynamics of the oxygen concentration distributions above the SWI have been analyzed as a function of organism density and in relation to their ventilation activity. The resulting mean oxygen gradients above the SWI were compared with the non-bioturbated case to investigate the effect of bioturbation on the oxygen transport mechanism.

Fig. 3.3: A). Picture of the experimental setup showing the four test tanks in the temperature-controlled water bath and the τLIF system consisting of laser and camera. B) Illustration of the projected laser light sheet from above and the illuminated area captured by the camera. The interrogation area was 14.4 × 19.2 mm^2. C) Typical burrow openings in the test tank. The image was taken in T1 before the start of the experiment. The dashed red line shows the location of the light sheet on the selected burrow opening.

Chapter 4

Discussions

4.1 τLIF oxygen imaging

This study successfully developed a new oxygen imaging system based on the lifetime-based laser induced fluorescence (τLIF) technique. For the first time, the spatial and temporal dynamics of oxygen concentration above the sediment surface in the presence of flow, natural organic sediments, and faunal activity can be quantified with high-spatial and -temporal resolutions. The τLIF system opens up a new horizon to study the insight on oxygen transport mechanism across the sediment-water interface in the presence of faunal activities.

Prior to this study, the benthic oxygen transport processes were studied by measuring the benthic oxygen flux and related it to the associated parameters of interests. The benthic flux was estimated using the benthic chamber (BC) method, the eddy correlation (EC) technique or by analyzing the thin boundary layer (TBL) on both sides of the sediment-water interface using oxygen microprofiler.

The EC technique has several advantages over the BC chamber method. First, it integrates fluxes from a larger contribution area than that of the benthic chamber. The flux contribution area depends on the flow velocity as well as flow direction. In a lentic system as observed in the Havel River measurements (Murniati et al., 2015), the flow directions were varied. For the observed bottom flow velocities in the range of 0.8 to 5.4 cm s^{-1}, it integrated an area of about 1 × 60 m, significantly larger than the dimension of the benthic chamber of the order less than 1 m^2 (Tengberg et al., 1995). Second, as a non-invasive technique it accounts for in-situ hydrodynamics condition. Third, it is able to measure the flux with a shorter temporal interval compared to that of the BC method. The temporal oxygen flux variation have been observed on time scales from minutes to days by Bryant et al. (2010a), Lorke et al. (2012) and (Brand et al., 2008) as well as in our study (Murniati et al., 2015).

However, while calculation of the total oxygen flux using the EC technique is relatively simple (Eq._1.12), it is derived from the assumptions of the stationarity and spatial homogeneity of turbulence and concentration gradients. Therefore, a relatively complex procedure has to be done to justify the basic assumptions, which are also dependent on the specific hydrodynamic conditions under which the measurements are performed, e.g., flux averaging time to include all relevant turbulent eddies and its stationarity and homogeneity (Lorke et al., 2013), oxygen production (Berg et al., 2013), steady flow (Holtappels et al., 2013), surface wave (Reimers et al., 2012), the distance of sampling volume to sediment surface (Rheuban & Berg, 2013) and response time and spatial alignment of the sensors (Donis et al., 2014). Additionally, if the benthic oxygen flux is considered as the sediment oxygen uptake rate, oxygen production between the sediment and the sampling volume of the sensors should be accounted. For this purpose, the parameters leading to oxygen production should also be collected, such as light penetration depth or chlorophyll a. In our study we examined the correlation between solar radiation and the resulting oxygen fluxes to assess the likely benthic oxygen production.

The TBL technique is the only technique that provides the insight on the oxygen transport process across the sediment-water interface by revealing the vertical oxygen concentration profile across the sediment-water interface in sub mm interval (Jørgensen & Des Marais, 1990; Jørgensen & Revsbech, 1985). The oxygen transport into the sediment is limited by the DBL, which its thickness and therewith the oxygen flux is modulated by bottom boundary layer turbulence (Lorke et al., 2012; Lorke et al., 2003; Murniati et al., 2015). While both BC and EC techniques estimate the total benthic oxygen flux, the TBL analysis can estimate the flux only if no fauna activity within the sediment is detected, which constantly or periodically changes the oxygen concentration at the vertical profile of interest. The difference between the flux estimates obtained from EC or BC techniques to that of the TBL analysis has been attributed to the benthic fauna activity (Archer & Devol, 1992; Glud, R.N. et al., 2003; Wenzhöfer & Glud, 2004).

The application of the τLIF system on bioturbation in this study gives us confidence on the suitability of the system to study the role of small-scale fluid mechanics, particularly the effect of benthic organism activities on the oxygen distribution above the sediment surface. It enables a more detailed analysis on the oxygen transfer mechanisms across the sediment-water interface, particularly in the presence of benthic organism activities. Below, we provide the detailed explanation on the τLIF system performance and its measurement uncertainty.

τLIF system performance

Oxygen sensitivity. We tested two types of oxygen indicators, i.e. platinum tetrakis-pentafluorophenyl phorphyrin (PtTFPP) and platinum octa-ethylphorpyrin (PtOEP), with two variants each. Macrolex Yellow (MY) with different concentrations were added to 3 out of 4 variants to enhance the luminescence intensity. In general, PtOEP has almost doubled oxygen sensitivity compared to that of PtTFPP, although in higher oxygen concentration (> 200 µmol L^{-1}), its sensitivity is similar to PtTFPP. Addition of MY increased the oxygen sensitivity. All the variants showed oxygen sensitivity ranging from 0 to 100% oxygen saturation. The lifetime variation indicated by standard deviation of the measured values (300-500 images) showed the variation of less than ± 2% of measurements. Similar variations in the lifetime of the oxygen indicator, however, resulted in different resolution in oxygen concentration. The oxygen resolution in higher oxygen concentration (~0.3 µmol L^{-1}) was slightly higher than that of in low oxygen concentration (~0.1 µmol L^{-1}). These characteristics make them highly attractive to be used in depleted oxygen environments.

Calibration curve. The lifetime-based LIF measurement principle makes the technique independent of oxygen indicator concentration and light distribution. Although the fluorescence intensity may decrease significantly during the experiments due to sedimentation and/or filtration of the fluorophore particles or photo-bleaching, calibration curve which is used to convert the lifetime into the oxygen concentration was not affected as long as the intensity threshold is exceeded. The τLIF performance experiments revealed an intensity threshold ~1250 for the oxygen concentration in the range of 0-100% oxygen saturation.

Temporal and spatial resolutions. As mentioned previously, the τLIF system has revealed an intensity threshold ~1250, i.e. if the image intensity of window 1 (W_1) is below this value, it will give incorrect oxygen estimates. To obtain a higher intensity, number of exposures/excitation cycles has to be increased, which in turn increases the lag time between W_1 and W_2. The lifetime method would yield inaccurate value if oxygen concentration changes drastically in between image acquisition of W_1 and W_2. This is seen as a bright spot around dark region or vice versa in the concentration image. Therefore, ideally, the lag time between the image acquisition of W_1 and W_2 should be as short as possible.

A small interrogation area at which increases the spatial resolution and the presence of natural organic sediments can reduce the light intensity. The distance of the light source to the interrogation area also contributes to the intensity level of the image. Placing the laser closer to the interrogation area from 25 cm to 10 cm above the water surface reduced the number of exposures from 45000 to 17000, thus increased the temporal resolution from 6 s to 2 s. The end result of the spatial resolution in the last setup was 12 µm per pixel. The intensity was gradually reduced during long-term measurements, particularly with sediments and *Chironomus plumosus* larvae. The reduction in intensity can be caused by light absorption by sediments, higher turbidity in the overlaying water, sedimentation, filtration of the nanobeads oxygen indicator or photo-bleaching.

The lifetime image always contains Gaussian distribution noise. Smoothing the fluorescence lifetime distributions using a low pass Gaussian filter reduces spatial resolution and removes peak concentration value. The variation (standard deviation) of the concentration estimates did not change significantly after applying the Gaussian filter with a 4 × 4-pixel (48 x 48 µm) window size.

Sediment-water interface detection analysis. The DBL thickness is in the order of sub millimeter and the sediment surface sometimes is not well defined. In microelectrode studies, the sediment-water interface was detected by slightly vibrating the sensor, where the surface was then defined when surface particles started to vibrate as well (Jørgensen & Revsbech, 1985) or by identification of the break in the oxygen gradient between the sediment- and water-sides (Boudreau & Jørgensen, 2001). Attempt to make an in-situ photograph capturing the sediment from above to detect the interface was short lived due to a focal depth camera resolution of 0.5-1 mm, which is insufficient to determine the location of the interface.

In this study, the camera was capturing the vertical pane including the sediment-water interface. A pronounced fluorescence intensity maximum caused by bottom reflection of the laser light and high bead concentration due to sedimentation have be observed. The vertical position of the SWI within the laser light sheet was detected as the local maximum in fluorescence intensity. Due to and depended on a combination of inclined sediment surface, the thickness of the light sheet and sedimentation of oxygen indicator on the sediment surface, the lower part of the vertical oxygen profile in the vicinity of the sediment-water interface might not be observed. For a laser light thickness of 1 mm with a 12° inclined sediment, an approximately 0.15 mm of the lower oxygen profile above the SWI should be truncated. To estimate the oxygen concentration at the SWI, the mean oxygen profile at the lower region is linearly extended to the SWI. It can also happen that locally elevated sediment surface located between the illuminated plane and the camera blocked the view on the actual sediment-water interface at the plane of interest. These regions should be excluded from the calculations.

Measurement uncertainty

The τLIF system represents a promising non-intrusive oxygen imaging technique, which is suitable for quantifying the two-dimensional oxygen concentration distributions and dynamics above the sediment-water interfaces in the presence of flow, natural organic sediments, and faunal activity. Sources of uncertainty are mainly resulted from: 1) high lag time between W_1 and W_2. If the time scale of the object of study is faster than the lag time of the instrument, i.e. if the concentration drastically changes during the image acquisition period of W_1 and W_2, 2) smoothing the lifetime image. Similar to other averaging methods, smoothing the lifetime image by Gaussian filter removes peak of concentration value. However, without filtering the image contains Gaussian noise. Fortunately, the noise can be removed with a relatively small window (a 4 × 4 pixel window), 3) inclined sediment. If the sediment is inclined and combined with the light sheet thickness, a portion of the vertical concentration profile in the vicinity of the sediment-water interface cannot be observed, 4) sediment working by animals. In the presence of sediment reworking by benthic animals, it may happen that locally elevated sediment surface located between the illuminated plane and the camera blocked the view on the actual sediment-water interface at the plane of interest, thus this region cannot be included in the vertical oxygen profile analysis, 5) nanobeads agglomeration. Even though that the nanobead diameter is less than 500 nm, it might happen that the beads are stacked by biofilms or sediment/organic particles and resuspended by the flow into the overlying water, which can be seen as speckles. Despiking algorithms using the phase space method is not adequate to remove the speckles due to the time lag or nanobeads coagulation.

The lag time can be reduced by two options: 1) Using a new setup: by increasing the output power of the laser, by changing the laser wavelength from 405 nm (the present setup) into 450 nm since the peak of the absorption of the oxygen indicator is at 450 nm or by using highly sensitive camera with the peak quantum efficiency at the emission wavelength of oxygen indicator in the range of 620 nm. 2) With the present setup: by increasing the image intensity to reduce the number of exposures by placing the laser as close as possible to the interrogation area, by decreasing the signal-to noise-ratio of the individual lifetime measurements, which could be accomplished by restricting the measurement range of oxygen concentration towards lower values.

4.2 Benthic oxygen flux

The net benthic oxygen flux across the sediment-water interface is controlled by sediment oxygen uptake rate and oxygen transport across the sediment-water interface. The benthic oxygen flux provides estimate of the sediment oxygen uptake rate if no oxygen production occurred. Aquatic systems are usually represented by physical characteristics, e.g. light, temperature, oxygen concentration, salinity, nutrients, hydrodynamic settings (waves, tides, flow or discharge, water depth) and habitat type (seagrass bed or marsh).

In our study, in situ measurements of the benthic oxygen flux using the EC technique were conducted in a riverine lake (cf. Fig. 3.2) during different seasons with the aims of investigating the controlling factors and quantifying the combined effects of hydrodynamic forcing and seasonal temperature on the sediment oxygen uptake rate. In steady-state condition, where sediment oxygen uptake rate is the same as oxygen transport across the sediment-water interface, the EC flux measurements provide an estimate of the benthic oxygen flux if no benthic primary production occurs.

The study confirmed that the benthic oxygen fluxes were most strongly correlated to bottom boundary layer turbulence which is driven by large-scale flows (Murniati et al., 2015). By using a simplified analytical model, which couples the effect of hydrodynamic forcing of the diffusive boundary layer with a temperature-dependent sediment oxygen uptake rate, we also confirmed that the flux is a non-linear function of a combined effect between friction velocity and temperature. Both friction velocity and temperature cause similar variability of the steady-state benthic oxygen flux.

Factors controlling benthic oxygen flux

The benthic oxygen flux can be considered as a proxy for mineralization rate (Glud, R.N. et al., 2016; Granéli, 1979a; Gudasz et al., 2010) thus for estimating the global carbon budgets (Seiter et al., 2005). The benthic oxygen flux has been investigated by estimating the oxygen transport rate (e.g. Lorke et al. (2003)) or by estimating the sediment oxygen uptake rate (e.g. Cai and Reimers (1995)). As mentioned before, from transport phenomena point of view, the benthic oxygen flux is predominantly controlled by boundary-layer turbulence driven by large-scale flows, while from the sediment oxygen uptake rate point of view, the benthic oxygen flux is controlled by availability of organic matters for decomposition. For both processes, the benthic oxygen flux has been correlated to various controlling factors, e.g. organic content, water depth, bottom water oxygen concentration, thickness of the diffusive boundary layers, fauna activity, light, temperature, sedimentation rates, trophic level and sediment permeability (Glud, R.N., 2008 and references therein). Some of those controlling factors are coupled, such as temperature, which influences both the transport processes and the sediment oxygen uptake rate.

In our study, we collected measured and derived physical variables, such as discharge, wind-speed, bottom water temperature, near-bed flow velocity, bottom oxygen concentration, turbulent kinetic energy dissipation rate and friction velocity as well as benthic oxygen fluxes. We observed short- (hourly) and long-term (seasonal) flux variations covering a wide range of those environmental conditions. The measured fluxes were varied both in short- and long-term scales.

Based on seasonal data, cross-correlations among measured and derived variables were statistically analyzed. Current velocity and water depth have been revealed as the most significant statistical predictors for the observed fluxes, which co-varied with discharge, temperature, and oxygen concentration. The range of variability of seasonal fluxes corresponded to the friction velocities and could therefore be attributed to the variability of hydrodynamic forcing. The strong correlation between the benthic oxygen flux and friction velocity is in accordance with many published in situ (Bryant et al., 2010a; Lorke et al., 2003) and laboratory measurements (Steinberger & Hondzo, 1999) as well as numerical simulations (Scalo, Carlo et al., 2012). The nearly linear relationship can be related to the modulation of the DBL thickness by boundary-layer turbulence (Lorke & Peeters, 2006), which is driven by large-scale flows in the respective aquatic system, such as internal seiche (Lorke et al., 2003) and due to backwater effect produced by a weir or hydropower operation (Lorke et al., 2012). Laboratory measurements have revealed the DBL and its thickness is largely influenced by flow velocity, which also coupled with the oxygen penetration depth into the sediment (Jørgensen & Des Marais, 1990). The water depth and benthic oxygen fluxes relationship might be attributed to the thickness of the DBL as well (Glud, R.N., 2008).

The hourly benthic oxygen fluxes also showed similar high variability as seasonal variations. Based on a theoretical analysis, Glud, R.N. et al. (2007) concluded that short-term, hydrodynamically driven flux variability does not affect long-term carbon mineralization rates or sediment oxygen uptake rates. This implies that short-term variations of waterside fluxes may result in non-steady-state conditions between sediment oxygen uptake and oxygen transport (Scalo, C. et al., 2013). While the long-term fluxes provide the mean sediment oxygen uptake rate, the short-term fluxes provide snapshots of the spatial and temporal variability of instantaneous benthic oxygen fluxes. The broader range of short-temporal flux may indicate that hydrodynamically driven oxygen transport rate might not be in equilibrium condition with sediment oxygen uptake rate, i.e. the sediment oxygen uptake rate may have different response time (=time constant) with the oxygen transport rate.

Coupled effect of temperature on net benthic oxygen flux

As mentioned before, some of the controlling factors, e.g. temperature, near-bed flow velocity, bottom oxygen concentration are intimately coupled. While flow is a predominantly the controlling factor for the oxygen transport, temperature controls both oxygen transport and consumption processes. Temperature can influence the oxygen transport processes by modifying the diffusivity D and oxygen solubility, while in the same time it can influence the sediment uptake rate by altering mineralization rates (Gudasz et al., 2010), internal nutrient cycle by zoobenthos (Fukuhara & Yasuda, 1985), benthic animals activity (Roskosch et al., 2012) and its abundance (Kajak, 1997).

The potential effect of temperature on oxygen fluxes were investigated using a simplified analytical model that combined the effect of hydrodynamic forcing of the diffusive boundary layer, which involves the temperature dependent molecular diffusivity D with a temperature-dependent oxygen consumption rate within the sediment. While the effect of temperature on oxygen solubility and on the diffusivity (molecular diffusion coefficient) D were not taken into account, the combined effects of temperature and friction velocity u_* to the flux results in a non-linear form. Over the seasonal range observed in our in situ measurements (4×10^{-4} m s^{-1} < u_* < 3×10^{-3} m s^{-1}, 8 °C < T < 21 °C), both factors cause similar variability of the steady-state benthic oxygen flux. Taking account only the dependency of temperature on the diffusivity, the oxygen transport will increase with increasing temperature. However, it can be offset by the reduction in oxygen solubility. By neglecting the effect of temperature on oxygen solubility, the temperature can cause a similar effect to the oxygen transport by modifying the diffusivity compared to the combined effect of temperature and flow velocity in the steady-state benthic oxygen flux. Unfortunately, the coupled effect of temperature on both oxygen transport and the sediment oxygen uptake was not investigated in this study (cf. **§ 5.2 Outlook Point 5**).

The combined effects of temperature and flow indicate that the expected increase of the benthic oxygen flux under climate change condition (Gudasz et al., 2010) can be offset by a reduction in flow velocity. A reduced of benthic oxygen transport into aquatic sediments in response to reduced flow velocity could ultimately lead to increasing carbon burial rates (Sobek et al., 2009) and in a growing importance of anaerobic mineralization pathways and increasing emission rates of methane (Maeck et al., 2013).

4.3 Biological induced benthic oxygen flux

As mentioned in the preceding section (**§ 4.1**), the τLIF system allows for studying the role of small-scale fluid mechanics generated by benthic organism activities on the oxygen distribution above the sediment surface. Hence it facilitates a more detailed analysis on the oxygen transport mechanisms across the sediment-water interface and therewith the biological induced benthic oxygen flux. The benthic oxygen flux provides estimate of the sediment oxygen uptake rate if no oxygen production occurred.

The ecosystem engineers have large effects on the physical and chemical processes occurring in the ecosystems (Hölker et al., 2015; Mermillod-Blondin, Florian & Rosenberg, 2006; Wright & Jones, 2006). The tube-dwelling animals, such as *C. plumosus* increase the oxygen availability in the sediment by drawing oxygen-rich water into the burrow which stimulates biogeochemical and microbial processes, while flushing of the burrow creates a three-dimensional flow field above the burrow which induces mixing. Application of the τLIF oxygen imaging system to investigate bioturbation caused by tube-dwelling animals of *C. plumosus* in our study confirms the potential importance of the biological controlling mechanism for benthic oxygen flux and therewith for nutrient and carbon cycling in aquatic ecosystems (Murniati et al., 2017). The advective transport of oxygen induced by burrow ventilation was the dominant transport mechanism.

Sediment oxygen uptake

Numerous studies have dealt with the effects of the benthic organism on the physical and chemical processes including nutrient cycling in aquatic sediments and overlying water (Andersson et al., 1988 and references therein; Fukuhara & Sakamoto, 1987; Granéli, 1979b). Burrow ventilation by tube-dwelling benthic animals introduces oxygen-rich water through a burrow inlet and releases plumes of deoxygenated water from a burrow outlet. The enhanced oxygen flux into the sediment stimulates aerobic respiration and is accompanied by enhanced exchange of solutes between sediment and overlying water (Fukuhara & Sakamoto, 1987; Hölker et al., 2015; Matisoff & Wang, 1998; Mermillod-

Blondin, F. et al., 2004). The enhancement of sediment oxygen uptake promoted by tube-dwelling benthic animals has been examined in numerous studies (Baranov et al., 2016b; Hansen et al., 1998; Hargrave, 1972a; Matisoff & Wang, 1998; Pelegri & Blackburn, 1996).

In accordance with previous observations for similar larval density of 2000 individuals m^{-2} (Baranov et al., 2016b; Polerecky et al., 2006; Soster et al., 2015), the areal oxygen uptake rates of the sediment increased up to 2.5-fold in the presence of chironomids. As there was no oxygen production occuring, the sediment oxygen uptake rate accounts for the oxygen transport rate. By assuming a respiratory oxygen demand of the organisms at the lower end of published data, the enhanced oxygen flux into the sediment exceeded the demand by up to a factor of 4, which confirms the potential importance of the prevailing controlling mechanism (physical versus biological) for mineralization rates and therewith for the nutrient and carbon cycling in aquatic ecosystems (Glud, R.N. et al., 2016; Granéli, 1979b; Hölker et al., 2015).

Biological induced oxygen transport

The *C. plumosus* larvae mostly spend their time inside the burrow and only very occasionally leave the burrow including for feeding purpose (Walshe, 1947 and personal observation). In the burrow they trap particles/planktons for feeding by constructing a conical net. Inside the burrow, they spend the time for conducting respiratory movement by undulating their body as sinusoidal wave (Brackenbury, 2000), feeding or making the net for feeding purpose. The movement of larva in the tube creates complex three-dimensional concentration distribution in the sediment (Lewandowski & Hupfer, 2005). The flow field observations using particle image velocimetry (PIV) revealed the existence of large-scale plumes, particularly at the burrow outlets (Morad et al., 2010; Roskosch et al., 2010). For the first time, the effect of these small-scale fluid mechanics on the oxygen concentration distribution and thus the DBL dynamics above the sediment-water interface could be quantified. These flows, which influence- the oxygen transport were generated by burrow ventilation. The turbulence was mainly generated by energetic plumes released from burrow outlets.

Burrow ventilation induced oxygen dynamics above the SWI. The τLIF application revealed distinct oxygen structures above the burrow inlet and outlet, which were associated with burrow ventilation. The pulse of energetic release of individual plumes from burrow outlet have clearly affected oxygen dynamics above the SWI. Occasionally, packages of water moving into the field of view from the side were observed, which were most likely advected by larger-scale flow structures from neighboring burrow outlets. Above the burrow inlet, the oxygen concentration distribution was less dynamic. Within a radius of 1-3 mm around the burrow inlet, the oxygen concentration was highly affected by the drawdown, whereas at larger distances from the opening the concentration was less dynamic and more homogeneous.

The spatial dimensions of the draw down zones above burrow inlets and of the released plumes above the outlets caused by the persistence of pumping-induced changes in the oxygen dynamics above the sediment water interface were principally in agreement with the measurements of the respective flow fields (Morad et al., 2010; Roskosch et al., 2010). Visual analysis of subsequently observed concentration distributions indicated that the plume velocities were mostly in the range of 0.6 to 2.1 mm s^{-1} with a maximum value of 4.8 mm s^{-1}, while using PIV technique Morad et al. (2010) have quantified a mean ventilation velocity of 15 mm s^{-1} with the maximum value at the center of the burrow outlet could be of 35 mm s^{-1}. The ventilation activity was characterized by pulsating flow with the duration of individual pumping event of about 2.5 min, where the *C. plumosus* larvae spent half of their time for ventilating the burrow. The ventilation activity is temperature and oxygen concentration dependent (Roskosch et al., 2012) as indicated by a negative trend of ventilation duration with oxygen concentration. At low oxygen concentration (~15 µmol L^{-1}), the ventilation duration was almost doubled.

The effect of advective transport during bioirrigation inside sediment matrix has been modeled by Brand et al. (2013). The effect of these flows to the transport of oxygen causing the DBL dynamics have been revealed in this study, which will be discussed below.

4.4 Oxygen transport mechanism

As mentioned in **§ 4.2.**, the benthic oxygen flux at waterside is predominantly controlled by boundary-layer turbulence, which is mostly generated by large-scale flow. The turbulence regulates the DBL thickness, i.e. its thickness is compressed by the higher magnitude of flow velocity (Jørgensen & Des Marais, 1990; Lorke & Peeters, 2006). The temporal mean vertical oxygen concentration profile in the DBL is characterized by a linear gradient (Jørgensen, 2001). The DBL region is, however, hydrodynamically unstable zone, which might be affected by the turbulent flows causing stochastic fluctuations of oxygen concentration. Both rapid and short residence time of turbulence driven variations in the DBL thickness make the DBL thickness a difficult parameter to resolve (O'Connor & Hondzo, 2008; Røy, H. et al., 2004). The effects of these hydrodynamic fluctuations for the benthic oxygen flux across the sediment-water interface under the influence of burrow ventilation are not well understood. Below we describe the effect of small-scale hydrodynamics induced by burrow ventilation to the DBL dynamics and benthic oxygen flux.

Diffusive boundary layer dynamics

As mentioned above, the persistence of pumping-induced changes in the oxygen dynamics above the sediment water interface have been observed, which is particularly generated by the energetic plumes released from burrow outlets. The instantaneous vertical oxygen concentration boundary layer was clearly degraded by the turbulence generated by burrow ventilation. The degraded temporal mean of the vertical oxygen concentration within a lateral radius of 2 mm above the opening of burrow outlet was also observed. This effect of burrow ventilation on the vertical oxygen concentration profile has also been found using planar optode causing a local oxygen increase within the aquatic sediments (Glud, R.N. et al., 1994; Wenzhöfer & Glud, 2004).

In the absence of burrow ventilation, the mean oxygen concentration profiles were characterized by two nearly linear sections, with the stronger vertical gradient within the lowest 1-3 mm above the SWI. Despite the broad range of temporal variability of the DBL thickness δ_{DBL} and oxygen concentration, the mean vertical oxygen profiles collapsed into a uniform shape within the diffusive boundary layer in a dimensionless presentation. In contrast to non-bioturbated case, the mean oxygen concentration profiles were degraded particularly by the energetic release of the deoxygenated plumes from outlets. The mean oxygen concentration gradients in the presence of animals decreased over time, whereas in the beginning of the experiments the thickness in bioturbated case was weaker.

Total and diffusive fluxes

Total benthic oxygen flux can be consisted of the diffusive and advective fluxes. In the absence of advective transport, the flux can be considered solely governed by molecular diffusion. The mass balance method, i.e. using the linear decreased of the oxygen concentration over time estimates the total flux. In non-bioturbated case, this method estimated the total flux of 10.8 mmol m^{-2} d^{-1}, while using the TBL analysis the threefold increase of the DBL thickness δ_{DBL} led to a corresponding decrease of the oxygen flux across the SWI from initially 12 to 3 mmol m^{-2} d^{-1} (cf. **§ 5.2 Outlook Point 2**). In the presence of burrow ventilation, the mass balance method gave total benthic fluxes of 10.1, 24.2, and 27 mmol m^{-2} d^{-1}, which increased with the increasing larval density from 612, 1224, and 2448 individuals m^{-2}, respectively.

The flux using the TBL analysis estimates the diffusive flux, where the oxygen transport closed to the interface is dominantly governed by molecular diffusion. Despite variability of the mean vertical oxygen gradients in the presence of burrow ventilation, applying this equation to the bioturbated cases revealed: 1) a consistent lower flux estimates compared to the total flux calculated by the mass balance method and lower than that of in the absence of burrow ventilation, 2) the flux estimate was decreasing with higher larval density. The flux estimates using the TBL method for the lowest larval density (612 individuals m^{-2}) was relatively constant throughout the measurements (6.2 ± 1.0 mmol m^{-2} d^{-1}), while the flux for the tank with larval density of 1224 individual m^{-2} was rather fluctuated (2.1 ± 1.2 mmol m^{-2} d^{-1}). In contrast, the diffusive flux for the highest larval density (2448 individuals m^{-2}) was close to zero. The preceding fluxes were estimated by including the advective transport by burrow ventilation, while the TBL technique assumes that the flux is solely governed by molecular diffusion. Therefore, these estimates tended to underestimate the local diffusive flux caused by degradation of the mean oxygen concentration gradients. The turbulence created by energetic release of the deoxygenated plumes induces mixing should, therefore, decrease the thickness of DBL and hence increases the magnitude of the local diffusive flux. Unfortunately, the burrow ventilation induced mixing and spatial flux variability have not been investigated in this study (cf. **§ 5.2 Outlook Point 3**).

The degraded concentration boundary layer and the fluxes estimates indicated that the advective transport by burrow ventilation is the dominant transport mechanism and the advective flux contribution to the total flux is increased with increasing larval density. While the difference between the diffusive oxygen fluxes estimated by the TBL analysis using oxygen microprofiler and the total benthic oxygen fluxes estimated either by the BC chamber or the EC method is correlated with the density of the benthic fauna (Glud, R.N. et al., 1994), the τLIF oxygen imaging application encompasses the analyses of the effects of fauna on the benthic oxygen fluxes.

4.5 Temporal variability of benthic oxygen flux

As mentioned in **§ 4.2**, the net transport rate of oxygen across the sediment-water interface is controlled by sediment oxygen uptake rate and oxygen transport across the sediment-water interface. As also discussed in **§ 4.2**, the measured benthic oxygen fluxes were varied both in short- (hourly) and long- (seasonal) terms. While the long-term fluxes provide the average sediment oxygen uptake rate, the short-temporal flux variability may indicate that sediment oxygen uptake and oxygen transport are not in steady-state conditions, which might be caused by different time scales between oxygen transport and sediment oxygen uptake. In previous section (**§ 4.3)**, we discussed the importance of benthic community on both oxygen transport and sediment oxygen uptake. Below we will discuss the time scale of the physical and biological factors and their interactions which affect the net oxygen flux.

Short-term and seasonal variabilities of physical factors

During in situ observations, a wide range of seasonal bottom water temperatures were observed, from 8.1 °C in the fall (Oct) to 21 °C in the summer (Aug), while during deployments the temperatures varied only slightly (the longest deployment was ~7 hours, max. temp – min. temp =0.4°C). In situ measurements of the near-bead flow velocity ranged from 8 to 54 mm s^{-1} (root mean squared of 3D flow field, measured at ~15 cm above the sediment). The seasonal temperature was co-varied with near-bed flow velocity and bottom water oxygen concentration. While the observed energetic release of the plume velocities from the burrow outlet were mostly in the range of 0.6 to 2.1 mm s^{-1} with a maximum value of 4.8 mm s^{-1}, quantification using PIV technique have revealed a mean ventilation velocity of 15 mm s^{-1} with the maximum value at the center of the burrow outlet could be of 35 mm s^{-1} (Morad et al., 2010), which is within the range observed in in situ measurements (cf. **§ 5.2 Outlook Point 4**).

Temporal dynamics of burrow ventilation

Individual pumping event lasted about 2.5 ± 1.5 min and larvae spent about 50 % of the time for active pumping. Pumping duration was most likely related to the oxygen concentration of the overlying water, which increased significantly when it is exposed to hypoxic condition. The oxygen concentration dependent of ventilation has also been observed by Roskosch et al. (2012). The pumping activity tends to be more active in warmer water temperature and low oxygen concentration. The flow velocity of the energetic release of plume from the outlet has been found to be higher than inflow to the burrow and depends on the life stage of *C. plumosus*, i.e. larval stage and pupa (Roskosch et al., 2010). The flow velocity caused by burrow ventilation of *C. plumosus* pupae was reduced to one-third compared to 4th instar larvae, from 15 mm s^{-1} to only 5.1 mm s^{-1} (Roskosch et al., 2010).

Benthic community density

The family Chironomidae is among the commonest and widest distributed freshwater insects, which its typical density is in the range of 70 to 11000 individuals m^{-2} (Hölker et al., 2015). Specifically for *C. plumosus*, the population density is mostly in the range of 1000 individuals m^{-2} (Granéli, 1979c), however, it can be up to 9000 individuals m^{-2} (Kajak, 1997). The life cycle of *C. plumosus* consists of the eggs, 4 larval instars, the pupa, and the adult. In aquatic sediment, the eggs hatch in 3-14 days, which depends on the bottom water temperature. The eggs hatch faster in warmer temperature and do not hatch below 8 °C (Hilsenhoff, 1966). Starting from 2nd instar, the larvae construct U-shaped tubes in the sediment and feed by the filter feeding method (Walshe, 1947). Larvae do net feed at sediment temperature below 5 °C and only above 12 °C the larvae feed actively (Hilsenhoff, 1966). During winter when the sediment temperature below 5 °C the larvae cease feeding thus remain in their larval stage. The duration of pupation is being dependent on the sediment temperature as well. At 24 °C the pupal stage could be last only 1 day, while 6-10 days is normal at 10 °C temperature. The emergence of *C. plumosus* from water normally starting about 1 hour before sunset and continuous into the night, even though it have also been observed throughout the days (Hilsenhoff, 1966).

The abundance of *C. plumosus* larvae in freshwater sediment is varied among locations and seasons, which mostly controlled by type of sediment, temperature of sediment, availability of organic matters and bottom water oxygen concentration (Pinder, 1986). The population density of *C. plumosus* in the sediment has been observed as winter maxima with the lowest during early summer (Jun-July), where the emergence of pupae started earlier in Apr-May (Hilsenhoff, 1966; Kajak, 1997; Maténa, 1989).

Interactions and temporal scale of physical-biological factors

The coupled physical-biological factors affecting the net benthic oxygen flux, i.e. the oxygen transport and the sediment oxygen uptake are shown in Fig. 4.1. While many factors can influence the benthic community population, in a simple representation the prominent factor that encompasses physical-biological factors for both oxygen transport and sediment oxygen uptake is temperature. In situ seasonal variation of flow showed that flow was co-varied with the temperature. Flow has a significantly positive impact on the oxygen transport. Lower temperature tends to decrease the burrow ventilation activity, which also affected by oxygen concentration condition. Hypoxic waters also increase the burrow ventilation activity (pumping duration) significantly. Larval density is at maximum in winter, however, only above 12 °C the feeding mechanism is fully active (Hilsenhoff, 1966). Temperature also controls larval development. Warmer water increases the rate of pupation, which negatively impacts the flow generated by burrow ventilation thus the oxygen transport. The larval density hits the lowest around summer. Lower oxygen transport by the flow coincides with higher temperature in the summer can be amplified by the reduced of benthic population density and pupation. However, it can be offset by the increased of ventilation activity. In contrast, lower temperature coincides with higher oxygen concentration, higher abundant of larvae and higher flow can be offset by lower activity of burrow ventilation. Investigation of the effect of the hydrodynamics on the oxygen transport alone suggested that the expected increase of the benthic oxygen flux under global warming can be offset by a reduction in flow velocity, which could ultimately lead to increasing carbon burial rates and in a growing importance of anaerobic mineralization pathways and increasing emission rates of methane.

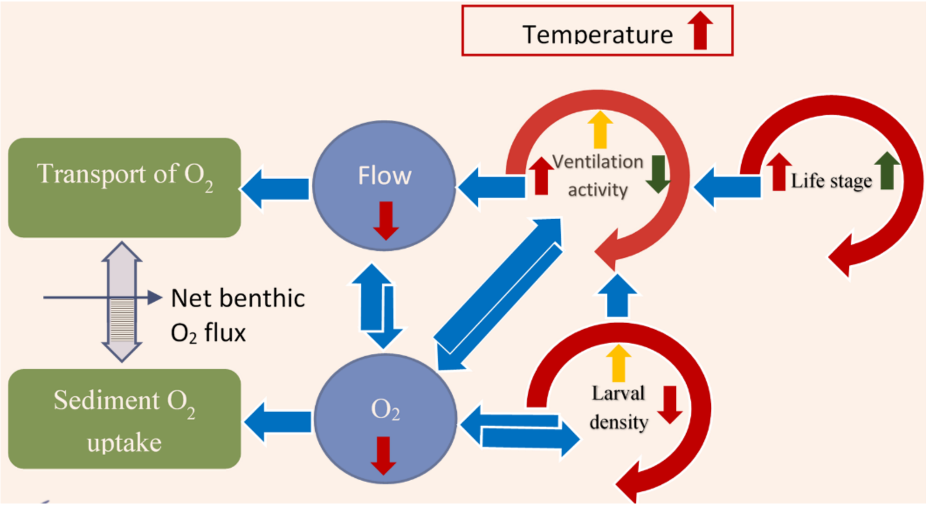

Fig. 4. 1: Diagram of physical-biological interactions affecting the net benthic oxygen flux. The same arrow color shows coupled interaction among variables, where up arrow shows an increase and down arrow shows a decrease. For example, the increase of life stage of the *C. plumosus* (green arrow), i.e. from larva to pupa, couples with a decrease in the ventilation activity. The increase of larval density (yellow arrow) will increase the ventilation activity. Temperature (red arrow) interacts with all variables, where the blue arrow shows the direction of its interactions. For example, a double headed arrow between oxygen concentration and ventilation activity shows that the ventilation activity depends on and at the same time affects the oxygen concentration of the overlying water. Explanation is provided in the text.

The biological effects on the net benthic oxygen flux variability have a mixed of the short- and seasonal time scales, where the biological effects on the sediment oxygen uptake rate most probably has a longer time scale (seasonal) than that to short-term scale (hourly/daily) oxygen transport. The broader range and a different time scale of the short-temporal flux may indicate that hydrodynamically driven oxygen transport rate might not in equilibrium conditions with sediment oxygen uptake rate (cf. **§ 5.2 Outlook Point 1**).

Chapter 5

Conclusions and outlook

5.1 Conclusions

The interactions between physical and biological factors that affect benthic oxygen flux across the sediment-water interface are elaborated in this thesis. The controlling factors that affect the variability of short- and long-term temporal scales of net benthic oxygen fluxes including the effects of burrow ventilation by tube-dwelling benthic animals on oxygen transport and sediment oxygen uptake have been examined. This study, for the first time is able to resolve the benthic diffusive boundary layer (DBL) dynamics using the newly developed lifetime-based laser induced fluorescence (τLIF) system which enables study of the role of small-scale fluid mechanics in the presence of benthic organism activity, and thus a more detailed analysis of mechanisms of oxygen transfer across the sediment-water interface. The τLIF system represents a promising non-intrusive oxygen imaging technique, which is suitable for quantifying two-dimensional oxygen concentration distributions and dynamics above the sediment-water interfaces in the presence of flow, natural organic sediments, and faunal activity (***Hypothesis 10***).

In-situ benthic oxygen fluxes show high variability in hourly and seasonal scales (***Hypothesis 2***). Statistical analysis reveal that current velocity and water depth are the most significant statistical predictors for benthic oxygen flux at the waterside, this co-varied with discharge, temperature, and oxygen concentration. The range of variability of seasonal fluxes corresponded to friction velocity, which is driven by large-scale flows (***Hypothesis 1***). Application of a simplified analytical model that couples the effect of hydrodynamic forcing of the diffusive boundary layer with a temperature-dependent oxygen consumption rate within the sediment showed that friction velocity and temperature cause similar variability of the steady-state benthic oxygen flux (***Hypothesis 3***).

The benthic oxygen flux can be influenced by fauna in two ways, i.e. by modulating the availability of oxygen that in-turn enhances sediment oxygen uptake, and also by enhancing the transport of oxygen. The areal oxygen uptake rates of the sediment increased up to 2.5-fold in the presence of tube-dwelling animals (***Hypothesis 4***). Oxygen transport rate was in excess of respiration by chironomids by up to a factor of 4.

The τLIF system application in bioturbation experiments facilitated the investigation of and provided insights into oxygen transport mechanisms across the sediment-water interface. Distinct oxygen structures above burrow inlets were revealed, these are associated with burrow ventilation (***Hypothesis 6***). The thickness of the DBL was dynamically changed (***Hypothesis 8***). In the absence of bioturbation, oxygen transport into the sediment is limited by the DBL, the thickness of which modulates the oxygen flux due to bottom boundary layer turbulence, which is in-turn driven by larger-scale flows in the respective aquatic system. This relationship, however, was completely altered by advective oxygen transport. Here the larger-scale mixing was generated by energetic plumes released at chironomid burrow outlets (***Hypothesis 7***). Despite DBL thickness variability in the presence of burrow ventilation, the diffusive flux estimates were consistently a small component to the total flux calculated by the mass balance method, and also less than that in the absence of burrow ventilation (***Hypothesis 5***). The diffusive contribution to the estimated total flux decreased with increasing larval density.

The temporal variability of net benthic oxygen flux had both short-term (hourly/daily) and seasonal components; sediment oxygen uptake rate most probably operates over the longer time scale, whereas oxygen transport operates at the short-term scale (***Hypothesis 9***). The broader range and different time scale of the short-term temporal flux may indicate that hydrodynamically driven oxygen transport rate is not in equilibrium conditions with sediment oxygen uptake rate.

The coupled physical-biological factors affecting net benthic oxygen flux can be represented by temperature as a prominent factor that encompasses physical-biological interactions for both oxygen transport and sediment oxygen uptake. The lower oxygen transport by the flow co-varied with higher temperature in the summer, and can be amplified by reduced benthic population density and pupation. It can also be offset by increased ventilation activity. In contrast, lower temperature which co-varied with oxygen concentration, higher abundance of larvae and higher flow, can be offset by reduced burrow ventilation activity. The expected increase in benthic oxygen flux under global warming could be offset by a reduction in flow velocity, which could ultimately lead to increased carbon burial rates and a growing importance of anaerobic mineralization pathways and increased methane emission rates.

5.2 Outlook

The τLIF oxygen imaging system represents a promising non-intrusive oxygen imaging technique, which is suitable for quantifying two-dimensional oxygen concentration distributions and dynamics above the sediment-water interface in the presence of flow, natural organic sediments, and faunal activity. From a technical point of view, there is still potential for improvement, such as reducing lag time and devising better algorithms for detecting the sediment-water interface and objects.

Some research questions are still open and new questions arose from this study:

1. Biological activity causes both short-term and seasonal scale temporal variations in net benthic oxygen flux; sediment oxygen uptake rate most probably operates at the longer time scale (seasonal), and oxygen transport at the shorter time scale (hourly/daily), this may result in non-steady-state conditions between sediment oxygen uptake and oxygen transport. While oxygen transport variability in this study spanned both timescales, however, that of sediment oxygen uptake (excluding from burrow ventilation activity) was not investigated in detail and the presence of non-steady conditions could not be confirmed in this study. In what circumstances is oxygen transport not in equilibrium with sediment oxygen uptake, and what are the driving factors leading to non-steady conditions?

2. The τLIF oxygen imaging application encompasses both total and diffusive flux measurements. While the flux estimates were continually decreased using the TBL method, the mass balance method provides a constant flux as long as the concentration change is linear. Since this study was conducted without significant background flow, for a more fundamental understanding of flux estimates by benthic chamber method, it may be interesting to investigate the effect of stirring on flux estimates. In in-situ measurements using benthic chamber, stirring has been adjusted to the thickness of the DBL outside the chamber to provide similar hydrodynamics inside the chamber (e.g. Glud, R.N. et al. (2003)). How does this stirring affect the flux measurement, apart from the DBL dynamics caused by the concentration gradient in the chamber itself?
3. The τLIF oxygen imaging methodology is able to estimate diffusive flux in the presence of burrow ventilation. In our study, we did not investigate spatial variation of fluxes, e.g., caused by various distances of the field of view of τLIF and the location of burrow openings (which cause small-scale hydromechanics by energetic release of the plumes). How does the distance to burrow outlets contribute to DBL dynamics and thereby to diffusive flux estimates?
4. PIV measurements have revealed that flows induced by burrow ventilation are within the range found in nature, and this study has revealed that advective transport is the dominant transport mechanism. The advective flux caused by burrow ventilation could therefore be the next phenomenon to investigate. How dominant is the advective transport in the presence of burrow ventilation compared to the large-scale turbulent in nature?
5. The schematic of physical-biological interactions affecting net benthic oxygen flux (Fig. 4.1) only shows a simple representation of the coupled effects controlling net benthic oxygen fluxes. How do coupled effects of overlying oxygen concentration and flow to oxygen transport in the presence and absence of burrow ventilation, contribute to the benthic oxygen flux dynamics at the waterside?

Given the potential significance of biological vs physical control of sediment–water fluxes, future investigators should aim at a more realistic representation of both processes and address mutual interactions of benthic boundary layer flow and bioirrigation. Based on above points, laboratory experiments are suggested to include: 1) advective flux estimation by simultaneous measurement of the flow field using the PIV technique, and oxygen concentration distribution using the τLIF imaging system (Point 2 and 4), 2) spatial variation assessment of the diffusive flux in the presence of burrow ventilation (Point 3), 3) observation of variation in temperature and oxygen concentration (Point 5), and temporal scale of the oxygen transport and sediment oxygen uptake in the presence of burrow ventilation (Point 1).

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Author’s contributions

This thesis is based on three research articles provided in Appendix A1-A3 which were composed by all the authors in each corresponding article. I was lead author in all articles. The contributions of the authors in each article are described in the following:

Appendix A1

Murniati, E., Geissler, S., et al. (2015). Short-term and seasonal variability of oxygen fluxes at the sediment–water interface in a riverine lake. *Aquat Sci, 77*(2), 183-196. doi:10.1007/s00027-014-0362-7

Conception and design : AL, EM
Data acquisition : EM, SG
Data processing & analysis : EM
Intrepretation of results : EM, AL
Writing the manuscript : EM, AL
Revising the manuscript : EM, SG, AL

Appendix A2

Murniati, E., Gross, D., et al. (2016). Oxygen imaging at the sediment-water interface using lifetime-based laser induced fluorescence (τLIF) of nano-sized particles. *Limnol Oceanogr Methods, 17*(8), 506-517. doi:10.1002/lom3.10108

Conception and design : AL, EM, DG, HH, KH, RNG
Instrument development & tests : DG
Data acquisition : EM, DG
Data processing & analysis : EM, HH
Intrepretation of results : AL, EM, HH, KH, RNG
Writing the manuscript : EM, AL
Revising the manuscript : AL, EM, DG, HH, KH, RNG

Appendix A3

Murniati, E., D. Gross, H. Herlina, K. Hancke, and A. Lorke. (2017). Effects of bioirrigation on the spatial and temporal dynamics of oxygen above the sediment-water interface. *Freshw Sci, 36*(4), 784-795. doi: 10.1086/694854

Conception and design : AL, EM, HH, KH, RNG
Instrument tests : DG
Data acquisition : EM, DG
Data processing & analysis : EM, HH
Intrepretation of results : AL, EM, HH, KH, RNG
Writing the manuscript : EM, AL
Revising the manuscript : AL, EM, DG, HH, KH

Author initial in alphabetical order

AL: Andreas Lorke
DG: Dieter Gross
EM: Erni Murniati
HH: Herlina Herlina
KH: Kasper Hancke
RNG: Ronnie Nøhr Glud
SG: Sebastian Geissler

Declaration

I hereby declare that the thesis entitled:

“Physical-biological interactions controlling the variability of oxygen flux across the sediment-water interface”

is the result of my own work except where otherwise indicated. It has not been submitted for any other degree at another university or scientific institution.

Landau in der Pfalz, 1 June 2017

Erni Murniati

Curriculum vitae

Erni Murniati

Date of birth	04.12.1975
Place of birth	Rajagaluh, Indonesia
Nationality	Indonesian
Email	murniati@uni-landau.de

Educational background

Since Oct 2011	Ph.D candidate in the Environmental Physics Working Group of the Institute for Environmental Sciences, University of Koblenz-Landau, Germany
Aug 2004 – Sep 2006	Master of Science (Resources Engineering) from the University of Karlsruhe (TH), Germany. Thesis: “Oxygen transfer dominated by buoyant convective instability in windless lakes”
Aug 1994 – Feb 1999	Bachelor of Civil Engineering from the Bandung Institute of Technology, Indonesia. Thesis: “Numerical study of the wind induced wave in a two-layer density stratified fluid using finite difference method”
Aug 1991 – Jun 1994	Senior High School 3 Bandung, Indonesia

Working experience

Dec 2000 – Oct 2011	Perum Jasa Tirta II, Jatiluhur, Indonesia
Jul 1997 – Dec 2000	Dinamaritama Engineering Consultant, Bandung, Indonesia

Awards

Aug 2017	Best talk award at the 5th Nereis Park Conference , USA
Jun 2011 – Sep 2014	DAAD/DIKTI Scholarship for doctoral degree program, Germany
Aug 2004 – Sep 2006	International Postgraduate Studies in Water Technologies (IPSWaT) scholarship, BMBF, Germany
Aug-Sep 2002	Operational Hydrology Course, SMHI/SIDA, Sweden

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Andreas, I could not ask for more. Thank you for your supports and your patience to answer my silly questions over and over again. Thank you for allowing me to have more time and get your fully supports to finish the degree. Thank you for your time and efforts and for understanding my writing and came up with a big leap to improve the manuscripts. I learn from the best.

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During my study time, I enjoy scientific as well as non-scientific discussions during breaks, lunch or anytime with people from AG Uphys, Zeyad, Lalith, Celia, Kaan and Andreas Mäck as well as from IfH, Christoph, Yulia, Sina, Katha, Alex, and Thibaud.

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Appendices

A1. In-situ O_2 flux measurements

This appendix has been published in the Aquatic Sciences journal with the following link:

Murniati, E., S. Geissler, and A. Lorke. (2015). Short-term and seasonal variability of oxygen fluxes at the sediment–water interface in a riverine lake. Aquatic Sciences, 77(2), 183-196. doi:10.1007/s00027-014-0362-7

A2. Development of τLIF system

Published manuscript

This manuscript has been published in the Limnology and Oceanography Methods journal with the following link:

Murniati, E., D. Gross, H. Herlina, K. Hancke, R. N. Glud, and A. Lorke. (2016). Oxygen imaging at the sediment-water interface using lifetime-based laser induced fluorescence (τLIF) of nano-sized particles. Limnology and Oceanography: Methods, 17(8), 506-517. doi:10.1002/lom3.10108

τLIF system

τLIF GUI for image acquisition (LabView) and τLIF Snapshot GUI (Matlab) are provided in a disc

A3. Imaging bioirrigation

This appendix has been published in the Freshwater Science journal with the following link:

Murniati, E., D. Gross, H. Herlina, K. Hancke, and A. Lorke. (2017). Effects of bioirrigation on the spatial and temporal dynamics of oxygen above the sediment-water interface. *Freshwater Science*, *36*(4), 784-795. doi: 10.1086/694854