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Alteration of *Chironomus plumosus* ventilation activity and bioirrigation-mediated benthic fluxes by changes in temperature, oxygen concentration, and seasonal variations

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Abstract. Burrowing benthic organisms promote water and solute fluxes across the sediment–water interface. Water and solutes penetrate the burrow walls and are transported into/out of the sediment when organisms flush their burrows with overlying water. Few studies have been done to investigate bioirrigation under shifting environmental conditions. We experimentally quantified bioirrigation by *Chironomus plumosus* larvae in the laboratory at 3 ranges of O_2 saturation (low, medium, and high O_2 concentrations), 2 temperatures (10 and 20°C), and over different seasons. We measured ventilation activities with O_2 and flow-velocity microsensors, flow velocities during pumping periods with color tracers, pumping rates with conductivity exchange experiments, and rates of advective and diffusive water influx into the sediment by influx assays (NaCl was the tracer in both latter experiments). O_2 saturations <12% extended pumping durations/h, whereas saturations <3% decreased pumping durations to ~0. Flow velocities were 2× higher when O_2 saturation was >50% than when it was <10%. Rising temperatures altered larval pumping (higher pumping frequency, lower pumping length) and increased flow velocity. Hence, pumping rate and rates of water influx were significantly higher at 20 than at 10°C. Seasonal variations in bioirrigation occurred despite constant laboratory conditions, i.e., the rate of water influx was significantly higher in spring/summer than in autumn. Our study shows that temporally varying environmental conditions should be considered when evaluating bioirrigation-mediated benthic fluxes across the sediment–water interface.

Key words: burrowing organisms, larvae, flow velocity, pumping rate, advective and diffusive water influx, endogenous clocks.

Burrowing benthic organisms enlarge the sediment surface area and promote active water transport across the sediment–water interface. Their ventilation activity, i.e., flushing their burrows with oxic water from the overlying water body (bioirrigation; Polerecky et al. 2006, Gallon et al. 2008) transports solutes and particulate constituents into the sediment pore water or back into the overlying water (Aller and Aller 1992, Aller 2001, Koretsky et al. 2002). Bioirrigation oxidizes the burrow walls, changes balances of redox reactions, and affects nutrient release or immobilization (Aller and Aller 1998, Lewandowski and Hupfer 2005, Meysman et al. 2006a). These changes influence microbial community structure in the sediment (Johnson et al. 1989, Stief et al. 2004, Bertics and Ziebis 2009) and chemical diagenesis (Andersson et al. 1988, Kristensen 2000, Stief and de Beer 2006). Thus, quantification of the benthic fluxes across the sediment–water interface induced by bioirrigating organisms is essential to understanding the microbiological and biogeochemical processes occurring in aquatic sediments (Boudreau and Marinelli 1994, Wang and van Cappellen 1996, Meysman et al. 2006b).

Quantification of bioirrigation-mediated benthic fluxes for a whole lake is difficult. First, the volumes of water pumped by diverse species differ greatly. Pumping rates between 1 and 16,000 mL h^{-1} $individual^{-1}$ have been reported (Kristensen 1983a, Leuchs

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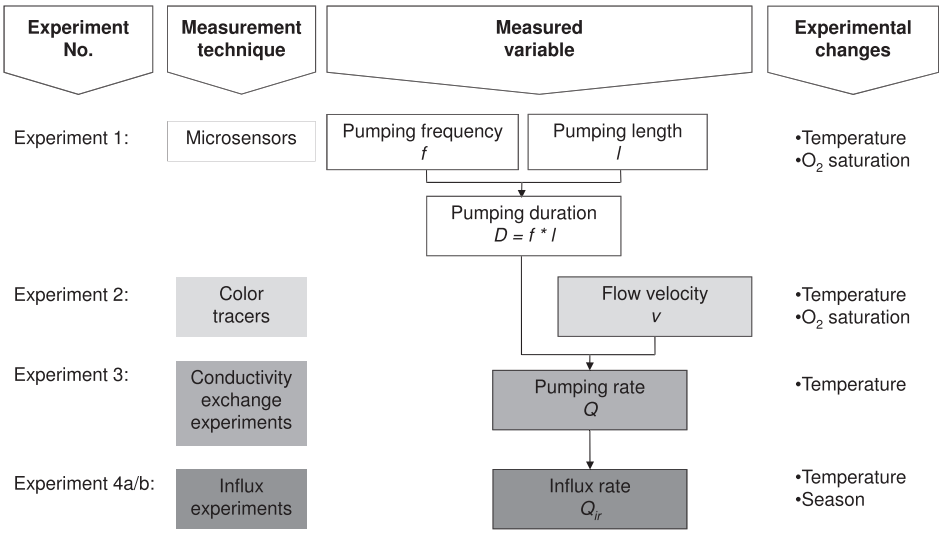

FIG. 1. Schematic diagram of the measurement techniques used for the 4 variables (experiment 1: pumping frequency, length, and duration; experiment 2: flow velocity; experiment 3: pumping rate; and experiment 4a, b: influx rate), and environmental variables that were manipulated in each experiment.

1986, Osovitz and Julian 2002). Population-wide pumping rates and, thus, quantification of bioirrigation-mediated fluxes depend on population densities. Moreover, fluxes are quite variable because pumping rates are susceptible to environmental biotic and abiotic conditions, such as food availability, presence of predators, and weather (Seymour 1972, Smethie et al. 2003, Hölker and Stief 2005). The response of benthic organisms to changes in temperature and O_2 concentration and the consequences for bioirrigation-mediated benthic fluxes, especially in freshwater sediments, have been investigated in few studies (Walshe 1948, Riisgård et al. 1992, Stief and Schramm 2010). Quantification of modified pumping rates under different environmental conditions is important because water temperatures and O_2 concentrations in freshwater lakes are expected to change in the future (Gerten and Adrian 2002, Wilhelm and Adrian 2008, Kirillin 2010).

Season also has a strong effect on benthic organisms and their activity. Dipteran larvae (Neumann 1965), algae, fish, and mammals (Lee and McClintock 1986, Grey et al. 2004, van Dijk et al. 2005) show seasonal and annual cycles of activity, emergence, growth, or fecundity even when they are kept at constant conditions in the laboratory. Results of a few studies suggest seasonal variations of benthic fluxes across the sediment–water interface (Hammond et al. 1985, Martin and Sayles 1987, Schlüter et al. 2000). However, ventilation activity and bioirrigation commonly are investigated under laboratory conditions without taking season into account. Consequently, alteration of benthic fluxes in response to the season is not completely understood and, especially for freshwater lakes, poorly investigated.

The aim of our study was to use innovative measurement techniques to evaluate ventilation activity (Roskosch et al. 2011) and bioirrigation-mediated benthic fluxes under experimental conditions mimicking shifting environmental conditions (Fig. 1). We conducted experiments with *Chironomus plumosus* (Diptera: Chironomidae) larvae, which build U-shaped tubes in muddy sediment (burrow length = up to 40 cm, depth = up to 20 cm; McLachlan and Cantrell 1976, Roskosch et al. 2010, 2011) and periodically pump water through the tubes by undulating body movements (Roskosch et al. 2010). Chironomidae occur in high densities (100–1000 larvae/m^2) in the profundal area of freshwater lakes (McLachlan 1977, Andersen and Jensen 1991, Kajak 1997). We hypothesized that changing O_2 concentrations and temperatures would alter ventilation activity (pumping frequency, length, and duration, and flow velocity) of *C. plumosus* larvae and result in significantly altered bioirrigation-mediated benthic fluxes (pumping rate and influx rate). We also hypothesized that seasonal variation caused by annual cycles would occur even if bioirrigation were measured under constant conditions in the laboratory.

Methods

Organisms, sediment, and water

We collected *C. plumosus* larvae from sediments at 6-m water depth at a fixed location (lat 52°44′N, long

13°65′E) from the shallow (mean water depth = 4.9 m), eutrophic, polymictic Lake Müggelsee in Berlin, Germany, approximately every 2 mo over 3 y (November 2007 to November 2010). We used 4th-instar (final-instar) larvae that were ~2 cm long and constructed burrows ~1.7 mm in diameter (Roskosch et al. 2011). We used sieved Lake Müggelsee sediment (1-mm mesh size) topped with Lake Müggelsee water for all experiments and for housing the larvae. Larvae began constructing burrows as soon as they were placed on sediments. Before the experiments, we kept larvae up to 1 wk in aerated tanks in darkness at 10°C without food.

Experiments

Experiment 1. Pumping frequency, length, and duration.—We measured the effects of O_2 concentrations and temperature on pumping frequency (number of periods of constant undulations/h), pumping length (time of constant undulations/period [s]), and pumping duration (total time spent ventilating/h [min/h]) with microsensors (1st hypothesis). We filled U-shaped Perspex tubes (20-cm length, 7-mm inner diameter) with sediment and fixed them in water-filled plastic tanks (261 ×160 ×172 mm, 10 tubes each) as described in Roskosch et al. (2010, 2011). We placed larvae at one end of a tube to guide their digging of a burrow along the tube to the other end. In contrast to other studies in which water-filled tubes were used (Walshe 1950, 1951, Kristensen 1983b, c), this arrangement allowed us to know burrow length while providing larvae with relatively natural conditions that did not alter their ventilation activity (Kristensen 1983a, Roskosch et al. 2011). We used 60 larvae (n = 60, 6 different tanks) per range of O_2 saturation and temperature. We acclimated larvae to the experimental conditions and allowed them to construct burrows for 2 d at the experimental temperature with constant aeration in darkness. Evaporation of water from the tanks was low, but if necessary, we replaced evaporated water with fresh lake water before the experiments were started.

We investigated the effects of low (0–3%), medium (>3–12%), and high (>12–100%) O_2 saturation on pumping frequency, pumping length, and pumping duration at 10 and 20°C. We chose these ranges of O_2 saturations to ensure that within-O_2-group responses were similar (see *Statistics* below). We gassed the tanks constantly with a mixture of N_2/CO_2 based on the partial pressure of the ambient air so that the pH was not affected by gassing. We covered the tanks with cling film to limit the redissolution of O_2 across the air–water interface. The different O_2 saturations were realized by altering the degree of gassing and covering the tanks. We checked O_2 concentration of the water continuously in the middle of the tank with O_2 microsensors (described below). Measurements were started 2 h after O_2 saturations were stable.

We investigated the effects of temperature at 10 and 20°C. We gassed the overlying water constantly with air (>>50% O_2 saturation) because we did not want limited O_2 to alter ventilation activity. The experimental temperatures corresponded to differences between spring/autumn (10°C) and summer (20°C) above-ground temperatures in Lake Müggelsee (R. Adrian, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, personal communication).

We measured pumping frequencies and lengths with Clark-type O_2 microsensors (OX-100, tip diameter = 50 or 100 µm; Unisense, Aarhus, Denmark) in burrow inlets and flow velocity microsensors (FS-25, tip diameter = 20 µm; Unisense Aarhus, Denmark; Revsbech et al. 1998, Brand et al. 2007) in burrow outlets as in Roskosch et al. (2011). Sensor tips were 2 mm deep in the middle of a burrow opening, and the start of a pumping period was indicated by simultaneous increases in O_2 concentrations and flow velocities caused by pumping of the larva. When ventilation activity stopped, O_2 concentrations decreased gradually, whereas flow velocities decreased instantly. We have no indication that the presence of microsensors affected ventilation activity behavior. *Chironomus plumosus* is a filter-feeder that usually dwells deep in its burrow and is not a surface-deposit feeder (Walshe 1951, Armitage et al. 1995). However, in few isolated instances, larvae detected the microsensors and built a new burrow tube beside the sensor tip. In such instances, only unaffected measurement periods were evaluated.

We calculated the arithmetic mean pumping frequency (f, /h) as the number of pumping periods divided by the length of the whole measurement time (average measurement time = 6 h). We estimated the arithmetic mean pumping length/period (l, /s) from all pumping periods during the whole measurement time. The mean pumping duration (D, min/h) was

$$D = fl \quad [1]$$

Experiment 2. Flow velocity.—We used color tracers to measure the effects of O_2 concentrations and temperatures on flow velocities (mm/s) within pumping periods (1st hypothesis). We used the same sediment-filled U-shaped Perspex tubes, tanks, and larval collection/acclimation procedure described for experiment 1. We conducted the experiment analogously to experiment 1 except that temperature measurements were done at slightly different O_2 saturations (low = 3–12%, medium = >12–30%, high

= >30–100%) because pumping length was extremely short when O_2 saturation was <3%, and reliable estimates of flow velocity were only possible for O_2 saturations >3%. Furthermore, the effect of O_2 concentration was investigated at 20°C only, whereas measurements in the range of high O_2 concentration (>>50%) were done at 10 and 20°C. We used 40 larvae (n = 40, 4 tanks) per O_2 group and temperature. We chose treatments based on statistical criteria as described for experiment 1.

We measured flow velocity with color tracers as described by Roskosch et al. (2011). We placed a dissolved color tracer (food color; Wusitta, Sitzendorf, Germany) with a pipette directly above the burrow inlet. When the larva started pumping, the tracer was sucked into the burrow. We immediately added a tracer of another color above the inlet. The time t (s) required for the 2nd tracer to become visible at the burrow outlet was timed with a stopwatch.

Assuming that the length l of the burrow (mm) built inside the Perspex tube was identical to the length of the Perspex tube, the flow velocity v (mm/s) of the color tracer during regular ventilation activity was

$$v = \frac{l}{t} \quad [2]$$

Experiment 3. Pumping rate.—We evaluated the effects of temperature (10 and 20°C) on pumping rates (mL/s) with conductivity exchange experiments (1st hypothesis). We fixed a sediment-filled Perspex tube (22-cm length, 7-mm inner diameter) in a water-filled plastic tank separated into 2 equal chambers (500 mL/chamber, 1 tube/tank, each end of the tube in a different chamber; see Roskosch et al. 2011 for details). We used 20 larvae and setups (n = 20, 20 tanks) per temperature, and allowed larvae to acclimate to the experimental conditions as described for experiments 1 and 2. We replaced evaporated water with fresh lake water before starting the experiments.

The measurements of the pumping rates were done as described in Roskosch et al. (2011). We used color tracers to distinguish the inlet and outlet of a burrow. Repeated measurements confirmed that larvae were always oriented in the same direction during pumping periods. We added 50 mg/L NaCl to the chamber that housed the burrow inlet and ensured uniform mixing of the water by constant aeration of both chambers. The limit of salinity tolerance for *C. plumosus* (NaCl = 10,000 mg/L) is much higher than the concentration used in experiment 3 (50 mg/L NaCl corresponding to an increase in electrical conductivity of ~100 µS/cm). The natural salinity of Lake Müggelsee is ~750 µS/cm, so it is very unlikely that the increased salinity affected ventilation activity (Lauer 1969). Equilibration of the tracer concentration in the inlet chamber was recorded continuously by conductivity meters (GMH3430; Greisinger Electronic, Regenstauf, Germany; accuracy = 0.5% but at least ±2 µS/cm) for 2 d. We connected the inlet and outlet chambers with a water-filled tube (diameter = 1 mm) to ensure constant water levels in both chambers.

We calculated the pumping rate Q (mL/h) based on an equation for the exchange between 2 compartments (Mutz et al. 2007). We estimated Q by minimizing the root mean squared error between the conductivity measured in the outlet chamber and the theoretical conductivity Lf_0 (µS/cm) at time t (h) based on the estimated Q. In the mass-balance equation 3, Lf_{Eq} (µS/cm) is the conductivity in each chamber at equilibrium, Lf_{start} (µS/cm) is the conductivity in each chamber at the start of the experiment, and V (mL) is the equal water volume in both chambers:

$$Lf_0(t) = exp\left(-2t\frac{Q}{V}\right)\left(Lf_{start}[t=0] - Lf_{Eq}\right) + Lf_{Eq} \quad [3]$$

Experiment 4a. Influx rate.—We evaluated the effect of temperature on the influx rates (= rate of advective and diffusive water influx of overlying water into the sediment [L/h]) (1st hypothesis). We filled round plastic columns (diameter = 59 mm) with sediment and water and added different densities of larvae (1 larva/column = 360 larvae/m^2, height (h)$_{sediment}$ = 10 cm, h_{water} = 5 cm; 10 larvae/column = 3600 larvae/m^2, $h_{sediment}$ = 15.5 cm, h_{water} = 15.5 cm). We chose this setup to assure almost natural conditions. The larvae were able to build their burrows freely in the sediment. The number of larvae corresponded to in situ abundances that are within the range normally found in eutrophic lakes (Svensson and Leonardson 1996, Kajak 1997).

We ran these experiments in batches (4 columns/date and temperature) in summer and autumn 2008 to 2010 (between July and November) (1 larva, 10°C, n = 24 columns; 1 larva, 20°C, n = 10 columns; 10 larvae, 10°C, n = 34 columns; 10 larvae, 20°C, n = 26 columns). We ran all influx experiments immediately after larvae, sediment, and water were sampled from Lake Müggelsee. We incubated columns for 2 d in darkness at 10°C so that larvae could build burrows and acclimate to the experimental conditions. On day 3, we raised temperatures to 20°C in ½ of the columns and allowed larvae to acclimate to the experimental temperatures for 1 d. We started measurements on day 4. We were focusing on the effect of temperature, but this effect could have been confounded by the effect of change in temperature. We aerated the

overlying water in all columns constantly. We replaced evaporated water with fresh lake water before the experiments were started.

To start, we removed ~10 mL of the overlying water and added NaCl dissolved in 10 mL of water (60 mg NaCl in experiments with h_{water} = 5 cm; 250 mg NaCl in experiments with h_{water} = 15.5 cm) to the laboratory column. The solution was mixed into the water column by aeration. We used the conductivity meters described above to record the decrease in NaCl in the overlying water caused by uptake of dissolved NaCl by the sediment for 7 d. We fitted the decrease in Lf_0 (μS/cm) and the influx rate Q_{ir} (L/h) with the mass-balance Eq. 3 described above (Mutz et al. 2007). However, in this experiment the volume of the overlying water V (mL) and the volume of the pore water V_{PW} (mL) had to be taken into account separately:

$$Lf_0 = \frac{\left(\left[exp\left(\frac{-t\,Q_{ir}(V+V_{PW})}{(V\,V_{PW})}\right)(Lf_{start}-Lf_{Eq})\right]+Lf_{Eq}\right)}{1000} \quad [4]$$

Experiment 4b. Influx rate under seasonal variation.—We measured advective and diffusive influx rates (L/h) with influx experiments conducted seasonally over a period of 3 y (2nd hypothesis). We used methods identical to those described for experiment 4a (10 larvae; 3600 larvae/m^2). We did the experiments at 10 and 20°C (n = 4 columns, 40 larvae/temperature and date, done on the same day) approximately every 2nd mo from November 2007 to November 2010 (18 dates for 10°C, 17 dates for 20°C). Experiment 4a for 10 larvae was a subset of experiment 4b (July to November).

Temperature coefficient.—We calculated the temperature coefficient (Q_{10}) from values measured at T_1 = 10°C and T_2 = 20°C as

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{\left(\frac{10}{T_2-T_1}\right)} \quad [5]$$

The rate (R) represents any measurement at both temperatures, T_1 and T_2. The Q_{10}-value illustrates the temperature dependency of pumping frequency, pumping length, pumping duration, flow velocity, pumping rate, and water influx. $Q_{10} > 1$ indicates that the variable increases, whereas $Q_{10} < 1$ indicates that the variable decreases with rising temperature.

Statistics

We measured pumping frequency, pumping length, flow velocity, and pumping rate at least twice per larva and obtained measurements for every larva that built tubes and ventilated them. By using a threshold approach we established boundaries for low, medium, and high O_2 saturation. Therefore, observations between >0 and 100% were grouped so that the group variance was minimized (groups with low standard deviations were chosen).

We did all statistical analyses with the statistical software SPSS (version 14; IBM Corporation, Montauk, New York). We used Shapiro–Wilk tests to check for normality of all variables within O_2 groups. We compared pumping frequency, pumping length, flow velocity, and pumping rate among O_2 groups with 1-way analysis of variance (ANOVA) if data were normally distributed or the nonparametric Kruskal–Wallis H-test if they were not. We used post hoc (Least Significant Difference or Dunnett-T3) or repeated 2-sample tests to assess differences in the contributions between each pair of O_2 groups. To compare 2 groups of values (e.g., between temperatures), we used Student's t-tests if distributions were normal and Mann–Whitney U-tests if they were not normal. The test and the p-value are reported when results were statistically significant ($p \leq 0.05$). If >2 measurement techniques were compared, we adjusted the p-value for significance with a Bonferroni correction.

Results

Effect of O_2

Experiment 1.—Ventilation activities (pumping frequency, length, and duration) differed significantly among O_2 groups (0–3% [low], >3–12% [medium], >12–100% [high]) at both temperatures (10 and 20°C). At 10°C, pumping frequency, length, and duration were significantly lower at low than at medium or high O_2 and did not differ significantly between medium and high O_2 (Table 1, Fig. 2A–C). However, pumping length and duration peaked at medium O_2, whereas pumping frequency did not differ appreciably between medium and high O_2. At 20°C, pumping frequency was significantly lower at medium than at high O_2 and did not differ between medium and low or between low and high O_2 (Fig. 2A). Pumping length and duration were significantly longer at medium than at low or high O_2 and significantly longer at high than at low O_2 (Fig. 2B, C). At low O_2, larvae conducted minor pumping (Fig. 3), but when O_2 saturation was <<2%, larvae almost stopped pumping.

Experiment 2.—Flow velocities measured within pumping periods at 20°C differed significantly among O_2 groups (3–12% [low], >12–30% [medium], >30–

TABLE 1. *p*-values for pairwise comparisons of pumping frequency, pumping length, and pumping duration among low, medium, and high O_2 saturation groups at 10 and 20°C (experiment 1) and for flow velocity among low, medium, and high O_2 saturation groups at 20°C (experiment 2). Superscripts indicate statistical test used to compare groups ([a] indicates analysis of variance, [b] indicates *t*-test, [c] indicates Mann–Whitney *U*-test). Bonferroni-corrected *p*-value for significance in all tests comparing a pair of groups was $p \leq 0.0167$.

Experimental conditions	*Experiment 1*			*Experiment 2*
	Pumping frequency	Pumping length	Pumping duration	Flow velocity
10°C	l < m: $p = 0.012$[a] l < h: $p = 0.011$[a]	l < m: $p < 0.001$[a] l < h: $p = 0.009$[a]	l < m: $p < 0.001$[a] l < h: $p = 0.001$[a]	
20°C	m < h: $p = 0.009$[a]	l < m: $p = 0.002$[a] l < h: $p = 0.001$[a] m > h: $p = 0.012$[a]	l < m: $p < 0.001$[a] l < h: $p < 0.001$[a] m > h: $p < 0.001$[a]	l < m: $p = 0.013$[b] l < h: $p < 0.001$[c] m < h: $p < 0.001$[c]
Low (l)	20 > 10: $p = 0.007$[b]			
Medium (m)			20 > 10: $p = 0.006$[b]	
High (h)	20 > 10: $p = 0.001$[b]	20 < 10: $p = 0.010$[b]		

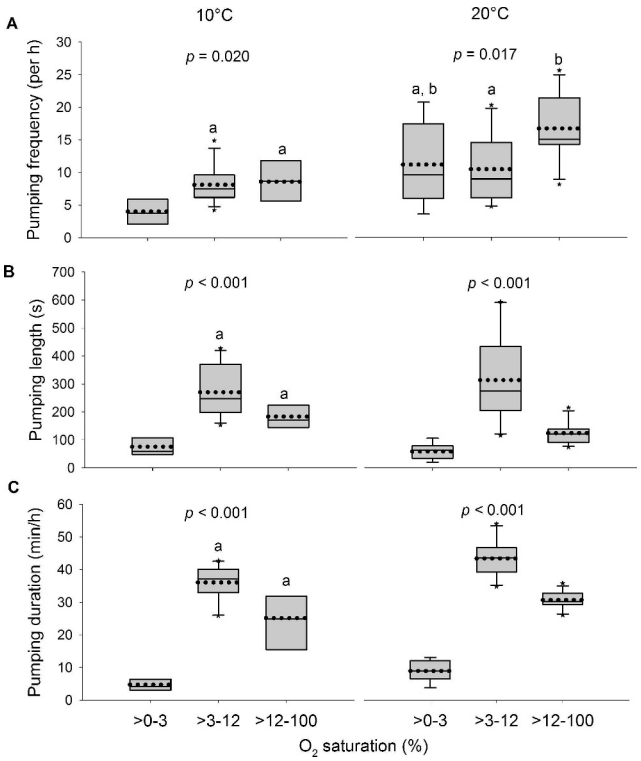

FIG. 2. Box-and-whisker plots for pumping frequency (A), pumping length (B), and pumping duration (C) of *Chironomus plumosus* larvae at 0 to 3% (low), >3 to 12% (medium), >12 to 100% (high) O_2 saturations at 10 and 20°C. Dotted lines indicate means, solid lines indicate medians, box ends are quartiles, whiskers show 2 standard deviations, and * indicates outliers. *p*-values indicate probabilities associated with 1-way analysis of variance done at each temperature (10 and 20°C) with O_2 group as the main effect (see Table 1 for post hoc comparisons of means and results of tests for differences between temperatures). Bars with the same letters are not significantly different.

100% [high]) and decreased with dropping O_2 concentrations (Table 1, Fig. 4).

Effect of temperature

Experiment 1.—Ventilation activity differed between temperatures. Pumping frequency was significantly higher at 20 than at 10°C (Fig. 5A), whereas pumping length was significantly lower at 20 than at 10°C (Fig. 5B). Pumping duration did not differ significantly between temperatures (Fig. 5C).

Experiment 2.—Flow velocity was significantly greater at 20 than at 10°C (Fig. 5D).

Experiment 3.—Constant pumping duration increased flow velocity at 20°C resulting in a significantly higher pumping rate at 20 than at 10°C (Fig. 5E). Q_{10}-values for all variables except pumping length and duration were >1 (Table 2).

Rate of water influx affected by temperature and seasonal variation

Experiment 4a.—The rate of advective and diffusive influx of overlying water into the sediment was affected by temperature at both larval densities. Q_{10}-values were 1.7 or 1.6, respectively, for experiments with 1 and 10 larvae (Table 2). We calculated per capita influx rate to provide a basis of comparison among experiments. Per capita influx rates were 1.7× (at 10°C) to 1.9× (at 20°C) higher at the lower than at the higher larval density (Fig. 6A, B). Originally, no comparison was planned between experiments, so experimental designs with 1 and 10 larvae differed slightly in terms of starting concentration of NaCl, sediment volume, and water volume, but sediment surface area was identical.

Experiment 4b.—Rates of water influx measured over 3 y under constant laboratory conditions were

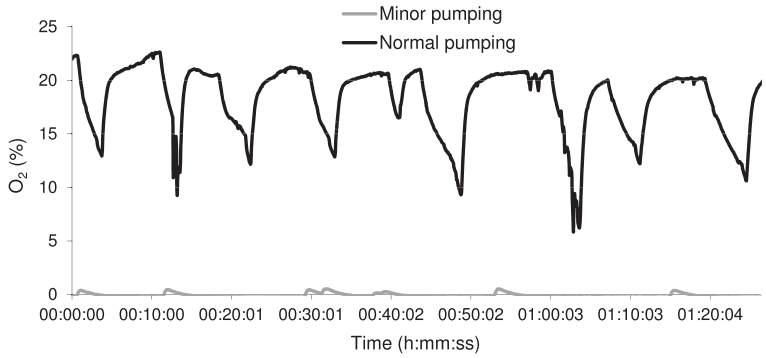

FIG. 3. Normal pumping at high O_2 saturation (>20%) and minor pumping at low O_2 saturation (<2%) measured by an O_2 microsensor in a burrow inlet (2 mm deep) in experiment 1. Data were taken from separate experimental trials. Time is coded as days, hours, and minutes.

significantly higher in spring/summer (April–July) than in autumn (September–October) (Fig. 7, Table 3). Across the entire period, the Q_{10}-value was 1.7.

Discussion

Effects of O_2 concentration, temperature, and season

Our results supported hypothesis 1. Larvae modified their ventilation activity, and thus, bioirrigation, in response to the O_2 concentration in the overlying water column (experiments 1 and 2). Our results suggest that larvae are able to balance a decrease in O_2 by increasing their pumping duration. At very low O_2 saturation, normal ventilation activity is minimized (Fig. 2A–C). We assume that in this case, O_2 consumption, which is necessary to perform pumping, exceeds O_2 gained by pumping. Some authors have described a switch to anaerobic metabolism for chironomid larvae in such almost-anoxic conditions (Augenfeld and Neess 1961, Nagell and Landahl 1978). At extremely low O_2 saturation, larvae pump slowly, rarely, and briefly, but regularly (Fig. 3). Without occasional ventilation activity, larvae presumably would be unable to assess the O_2 concentration of the overlying water, and thus, would not register a renewal of O_2, should it occur. In our experiments, ventilation activity stopped when the O_2 saturation in the overlying water decreased to <<2%. In addition, the O_2 concentrations in the burrow adjacent to the larvae are probably even lower because O_2 saturation decreases further when the water from the surrounding anoxic sediments flows through the burrow. Walshe (1950) also reported that *C. plumosus* pumping length increased as O_2 concentrations decreased and that pumping length decreased drastically when O_2 was <5% (cf. <3% in our study). *Chironomus thummi*, another bioirrigating larva occurring in shallow lakes, increased pumping length and pumping duration as O_2 concentrations decreased (Leuchs 1986). In contrast to our study, the pumping frequency did not decrease with dropping O_2 concentrations in either of these studies. Both studies were done with larvae in water-filled tubes with a diameter wider than natural burrows. Such tubes are known to alter bioirrigation (Kristensen 1983a, Roskosch et al. 2010). In our study, tubes were filled with sediment. Roskosch et al. (2010, 2011) showed that results from burrows built in sediment-filled tubes were not significantly different results from burrows built directly in the sediment.

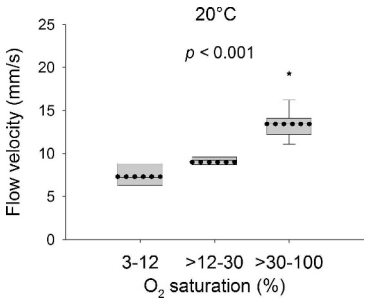

FIG. 4. Box-and-whisker plot for flow velocity of *Chironomus plumosus* larvae at 3 to 12% (low), >12 to 30% (medium), and >30 to 100% (high) O_2 saturations measured at 20°C in experiment 2. Dotted lines indicate means, solid lines indicate medians, box ends are quartiles, whiskers show 2 standard deviations, and * indicates outliers. Data were analyzed with a Kruskal–Wallis *H*-test (see Table 1 for *p*-values). Bars with the same lower case letter are not significantly different.

Our results confirmed that water temperature affects bioirrigation of *C. plumosus* significantly and temperature changes result in modified ventilation activity and pumping rates (Experiments 1, 2, and 3). Presumably this change in activity with temperature is explained by the fact that the larvae are poikilotherms

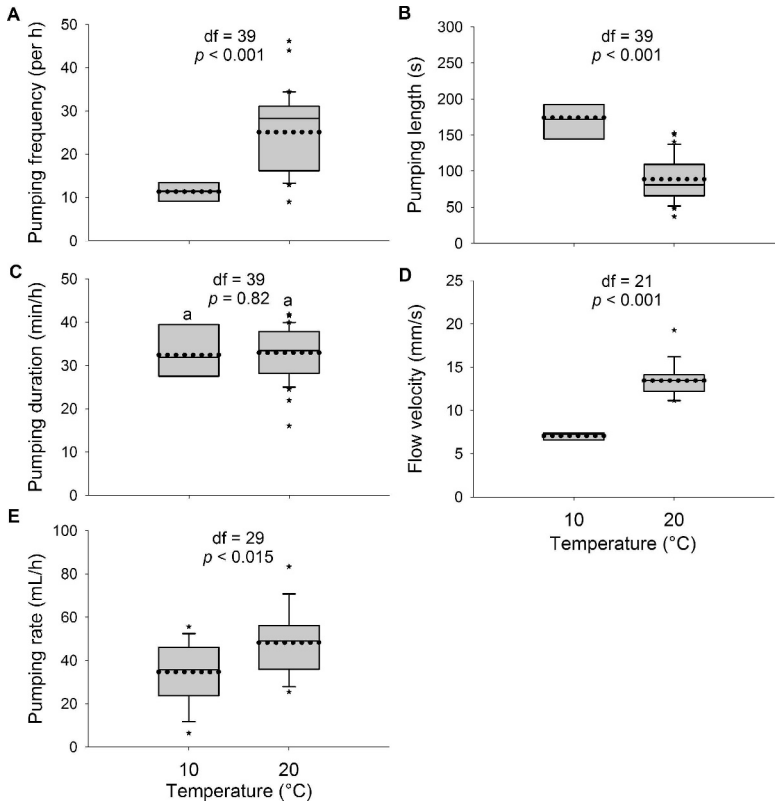

FIG. 5. Box-and-whisker plots for pumping frequency (A), pumping length (B), pumping duration (C), flow velocity (D), and pumping rate (E) of *Chironomus plumosus* larvae at 10 and 20°C under high O_2 concentrations (>>50%) in experiments 1 to 3. Dotted lines indicate means, solid lines indicate medians, box ends are quartiles, whiskers show 2 standard deviations, and * indicates outliers. Data were analyzed with *t*-tests. Bars with the same lower case letter are not significantly different.

(Platzer 1967, Pinder 1986). Change in pumping frequency and length with temperature is consistent with results of studies on bioirrigating worms (Seymour 1972, Kristensen 1983c) and larvae (Walshe 1950, Leuchs 1986). However, Leuchs (1986) reported that the increased pumping rate of *C. thummi* with temperature was the result of a longer pumping duration, and not of increased flow velocity in the burrows as occurred in our study. The discrepancy may result from differences in the feeding behavior of the 2 species. *Chironomus plumosus* is a filter-feeder that catches particles from the water flowing through its burrow in a conical net (Walshe 1950, Armitage et al. 1995), whereas *C. thummi* is a deposit-feeder. Roskosch et al. (2010) showed that filter feeding increases the pumping rate substantially because a larva pumps for respiration and to meet its food requirements. Therefore, depending on the available food quantity, filter-feeders must pump a considerable amount of water through their burrows (Walshe 1951, Nielsen et al. 1995, Riisgård and Larsen 2005). When larvae ventilate their burrows with a faster flow velocity, the net is more quickly packed with particles. Hence, we assume that rising temperatures might result in shorter pumping periods of *C. plumosus*.

The rate of advective and diffusive water influx into the sediment was significantly altered by rising temperatures (Experiments 4a, b). The Q_{10}-values (1.6–1.7; Table 2) confirmed that larval activity was modified by temperature changes (Naylor 1963). Our results concur with those from a previous study indicating that bioirrigation affects the pore-water composition more strongly in warm summer (up to 22°C) than in cold winter (down to 5°C) (Martin and Sayles 1987). Seasonal variation of bioirrigation-mediated benthic fluxes were assumed in a few in situ studies (Hammond et al. 1985, Schlüter et al. 2000, Smethie et al. 2003).

Our measurements of influx rates support the hypothesis that seasonal variation (circumannual cycling) occurs even if bioirrigation is measured when laboratory conditions, such as O_2 supply or temperature, are constant (experiment 4b). We kept experimental conditions constant during the 3-y study, but rates of water influx into the sediment (spring/summer vs autumn) clearly differed between seasons.

TABLE 2. The temperature coefficient (Q_{10}) for pumping frequency, pumping length, pumping duration, flow velocity, pumping rate, and rate of water influx at 10 and 20°C.

	Experiment 1			Experiment 2	Experiment 3	Rate of water influx		
10:20°C	Pumping frequency	Pumping length	Pumping duration	Flow velocity	Pumping rate	Experiment 4a (1 larva)	Experiment 4a (10 larvae)	Experiment 4b
Q_{10}	2.3	0.5	1.0	1.9	1.4	1.7	1.6	1.7

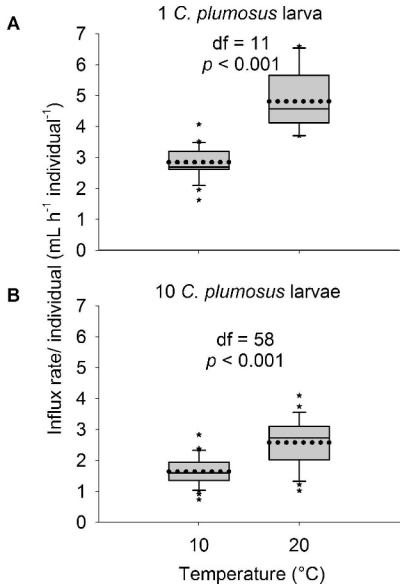

FIG. 6. Box-and-whisker plots for rate of advective and diffusive water influx into the sediment per individual caused by pumping of *Chironomus plumosus* larvae at the individual (1 larva = 360 larvae/m^2; experiment 4a) (A) and population level (10 larvae = 3600 larvae/m^2; experiment 4b) (B) at 10 and 20°C. Experiment 4a was done in summer and autumn 2008, whereas experiment 4b was done in summer and autumn 2008, 2009, and 2010 (July to November each year). Dotted lines indicate means, solid lines indicate medians, box ends are quartiles, whiskers show 2 standard deviations, and * indicates outliers. Data were analyzed with *t*-tests. Bars with the same lower case letter are not significantly different.

Such seasonal variability under constant conditions might occur if larvae had endogenous clocks responsible for the variations occurring in the laboratory. Circumannual cycles have been reported as a source of variability in other laboratory experiments. For instance, in a study of fish (juvenile roach, *Rutilus rutilus*) van Dijk et al. (2005) found significant differences in physical variables between summer and winter although laboratory temperatures were constant. Endogenous clocks or circumannual cycles also are known from studies of other insects, algae, cyanobacteria, and *Daphnia* populations kept at constant temperature, food availability, and photoperiod in the laboratory (Neumann 1965, Kao et al. 2010; N. Bauer, C. Dziallas, D. Baganz, and G. Staaks, Leibniz Institute of Freshwater Ecology and Inland Fisheries, personal communication). However, studies of the effects of endogenous clocks on ventilation activity and bioirrigation-mediated benthic fluxes, especially in freshwater sediments, are scarce (Saunders et al. 2004). Pumping rates are commonly determined under laboratory conditions without

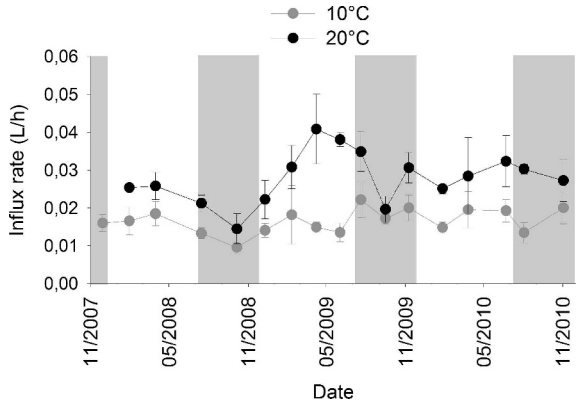

FIG. 7. Mean (±1 SD) rate of advective and diffusive water influx into the sediment caused by the pumping of a *Chironomus plumosus* population (10 larvae = 3600 larvae/m^2) at 10 and 20°C during the 3-y study (experiment 4b). Experiments in grey boxes were conducted in summer and autumn 2008, 2009, and 2010 and were used to compare the rate of water influx into the sediment caused by pumping of *C. plumosus* larvae at 10 and 20°C.

taking the season into account. Our results indicate that seasonal variations of bioirrigation should be considered carefully in future experiments. The major part of our experiments was conducted in summer to autumn 2008 because it was technically impossible to conduct all experiments at the same time. Thus, a part of the variability observed in our experiments might be attributable to seasonal variations.

Advanced environmental implications

A quantitative evaluation of bioirrigation-mediated benthic fluxes and their alterations is essential to understanding the biogeochemical processes in aquatic sediments and for applying dynamic diagenetic models (Boudreau and Marinelli 1994, Wang and van Cappellen 1996). Predictive modelling is becoming increasingly important because environmental conditions, such as water temperature and O_2 concentrations, are shifting rapidly with global climate change. For example, long-term measurements of the water temperature of Lake Müggelsee show that its mean annual temperature has been increasing by ~0.3°C per decade (Kirillin 2010). Moreover, Kirillin (2010) predicted that mixing patterns in the shallow lake eventually will change from polymictic (mixed water column) to dimictic (stratification periods in summer and winter) and, finally, to warm monomictic (no winter stratification, strong stratification in summer). Consequently, the hypolimnetic O_2 concentration will decrease because warmer temperatures and earlier diatom spring blooms will lead to a higher mineralization rate, especially at the lake bottom (Wilhelm and Adrian 2008). In Lake Müggelsee, O_2 saturation in the hypolimnion (measured directly above the sediment, 5-m water depth) usually does not decrease below 25% (R. Adrian, personal communication). However, during short-term stratification periods in summer, low O_2 saturation (<2 mg/L) may occur (Wilhelm and Adrian 2008). In the future, stratification periods are expected to become longer (Kirillin 2010). Our results indicate that under such low O_2 conditions, ventilation activity will be affected and pumping rate of *C. plumosus* larvae in Lake Müggelsee will decrease significantly.

Pumping rates and, thus, bioirrigation-mediated benthic fluxes are affected by population density. Mean larval density over 3 y in Lake Müggelsee was 514 ± 299 (n = 20) 4th-instar *C. plumosus* larvae/m^2 sediment (Roskosch 2011). Assuming this abundance remains constant all year and that *C. plumosus* is the only bioirrigating species in the lake, a change in temperature from 10 to 20°C would yield a 40% increase (Q_{10} = 1.6–1.7; Table 2) in the population-wide pumping rate (from 430 to 600 L m^{-2} d^{-1}, based on rates of 34.7 and 48.3 mL h^{-1} individual^{-1}, respectively). Given the volume of Lake Müggelsee (3.65×10^9 L), this rate implies that the equivalent of the volume of the entire lake is pumped through the sediment in 10.4 d at 20°C instead of 14.4 d at 10°C (Roskosch et al. 2010). This extrapolation is only an approximation of the in situ pumping rate, but the values confirm the strong effects of bioirrigation on the aquatic environment.

Water influx into the sediment per individual decreased with increasing abundance of larvae (experiment 4a with 360 and 3600 larvae/m^2 sediment). The efficiency per larva decreased with increased abundance by a factor of 0.58 in our experiments. McLachlan (1977) reported that *C.*

TABLE 3. Mean (±1 SD; median in parentheses) spring/summer (April–July) and autumn (September–October) advective and diffusive water influx (mL/h) into the sediment measured for 10 larvae at 10 and 20°C.

Season	10°C	20°C
Spring/summer	17.0 ± 4.2 (16.0); n = 24	31.9 ± 9.0 (31.1); n = 24
Autumn	12.7 ± 3.6 (12.0); n = 12	22.3 ± 7.8 (21.7); n = 10
Spring/summer > autumn	t-test: p = 0.020; df = 34	t-test: p = 0.006; df = 32

plumosus kept at very high densities build shorter tubes. Consequently, water influx into the sediment depends not only on the pumping rate, but also on variables, such as community composition, burrow shape (I-, U-, Y- or branched tubes), and burrow dimension (effective exchange surface) (Graneli 1979, Koretsky et al. 2002). Hence, the influx rate per individual might be lower at densities >3600 larvae/m^2. Bioirrigation-mediated fluxes at the sediment–water interface are highly sensitive to environmental conditions, population density, tube dimensions, and sediment physics (permeability and porosity, muddy or sandy sediment) (Meysman et al. 2006a, b). Bioirrigation-mediated benthic fluxes should be quantified under different environmental conditions and for diverse species and sediments.

O_2 concentration, temperature, and season alter ventilation activity and advective and diffusive water influx into the sediment. As O_2 concentration dropped, pumping duration increased and subsequently decreased, whereas flow velocity constantly decreased. As temperature rose, pumping duration remained the same, whereas flow velocity increased. Thus, changing conditions led to changes in pumping rates. Moreover, the rate of water influx was always higher in spring/summer than in autumn. This result shows that the season should be considered even when test organisms are brought into the laboratory and bioirrigation measurements are done under laboratory conditions. For meaningful quantification of bioirrigation-mediated benthic fluxes, measurements must be made carefully and under precise experimental conditions, especially when the data are being interpreted or extrapolated to population-scale rates.

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Literature Cited

ALLER, R. C. 2001. Transport and reactions in the bioirrigated zone. Pages 269–301 *in* B. P. Boudreau and B. B. Jorgensen (editors). The benthic boundary layer. Oxford University Press, New York.

ALLER, R. C., AND J. Y. ALLER. 1992. Meiofauna and solute transport in marine muds. Limnology and Oceanography 37:1018–1033.

ALLER, R. C., AND J. Y. ALLER. 1998. The effect of biogenic irrigation intensity and solute exchange on diagenetic reaction rates in marine sediments. Journal of Marine Research 56:905–936.

ANDERSEN, F. O., AND H. S. JENSEN. 1991. The influence of chironomids on decomposition of organic matter and nutrient exchange in a lake sediment. Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie 24:3051–3055.

ANDERSSON, G., W. GRANÉLI, AND J. STENSON. 1988. The influence of animals on phosphorus cycling in lake ecosystems. Hydrobiologia 170:267–284.

ARMITAGE, P., P. S. CRANSTON, AND L. C. V. PINDER. 1995. The Chironomidae: biology and ecology of non-biting midges. Chapman and Hall, London, UK.

AUGENFELD, J. M., AND J. C. NEESS. 1961. Observations on the respiratory enzymes of various life-stages of *Chironomus plumosus*, *Chironomus stageri*, and *Aedes aegypti*. Biological Bulletin 120:129–139.

BERTICS, V. J., AND W. ZIEBIS. 2009. Biodiversity of benthic microbial communities in bioturbated coastal sediments is controlled by geochemical microniches. ISME Journal 3:1–17.

BOUDREAU, B. P., AND R. L. MARINELLI. 1994. A modelling study of discontinuous biological irrigation. Journal of Marine Research 52:947–968.

BRAND, A., B. MÜLLER, A. WÜEST, AND C. DINKEL. 2007. Microsensor for in-situ flow measurements in benthic boundary layers at sub-millimeter resolution with extremely slow flow. Limnology and Oceanography: Methods 5:185–191.

GALLON, C., L. HARE, AND A. TESSIER. 2008. Surviving in anoxic surroundings: how burrowing aquatic insects create on oxic microhabitat. Journal of the North American Benthological Society 27:570–580.

GERTEN, D., AND R. ADRIAN. 2002. Effects of climate warming, North Atlantic Oscillation and El Niño on thermal conditions and plankton dynamics in European and North American lakes. TheScientificWorld 2:586–606.

GRANELI, W. 1979. The influence of *Chironomus plumosus* larvae on the oxygen-uptake of sediment. Archiv für Hydrobiologie 87:385–403.

GREY, J., A. KELLY, S. WARD, N. SOMMERWERK, AND R. I. JONES. 2004. Seasonal changes in the stable isotope values of lake-dwelling chironomid larvae in relation to feeding and life cycle variability. Freshwater Biology 49:681–689.

HAMMOND, D. E., C. FULLER, D. HARMON, B. HARTMAN, M. KOROSEC, L. G. MILLER, R. REA, S. WARREN, W. BERELSON, AND S. W. HAGER. 1985. Benthic fluxes in San Francisco Bay. Hydrobiologia 129:69–90.

HÖLKER, F., AND P. STIEF. 2005. Adaptive behaviour of chironomid larvae (*Chironomus riparius*) in response to chemical stimuli from predators and resource density. Behavioral Ecology and Sociobiology 58:256–263.

JOHNSON, R. K., B. BOSTRÖM, AND W. VAN DE BUND. 1989. Interactions between *Chironomus plumosus* (L.) and the

microbial community in surficial sediments of a shallow, eutrophic lake. Limnology and Oceanography 34:992–1003.

KAJAK, Z. 1997. *Chironomus plumosus*—what regulates its abundance in a shallow reservoir? Hydrobiologia 342/343:133–142.

KAO, C.-C., J. CHEN, G.-F. CHEN, AND K. SOOG. 2010. Variable swarming time of an intertidal midge (*Pontomyia oceana* Tokunaga, 1964) controlled by a circadian clock and temperature. Marine and Freshwater Behaviour and Physiology 43:1–9.

KIRILLIN, G. 2010. Modeling the impact of global warming on water temperature and seasonal mixing regimes in small temperate lakes. Boreal Environment Research 15: 279–293.

KORETSKY, C. M., C. MEILE, AND P. VAN CAPPELLEN. 2002. Quantifying bioirrigation using ecological parameters: a stochastic approach. Geochemical Transactions 3:17–30.

KRISTENSEN, E. 1983a. Comparison of polychaete (*Nereis* spp.) ventilation in plastic tubes and natural sediment. Marine Ecology Progress Series 12:307–309.

KRISTENSEN, E. 1983b. Ventilation and oxygen uptake by three species of *Nereis* (Annelida: Polychaeta). I. Effects of hypoxia. Marine Ecology Progress Series 12:289–297.

KRISTENSEN, E. 1983c. Ventilation and oxygen uptake by three species of *Nereis* (Annelida: Polychaeta). II. Effects of temperature and salinity changes. Marine Ecology Progress Series 12:299–306.

KRISTENSEN, E. 2000. Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals. Hydrobiologia 426:1–24.

LAUER, G. J. 1969. Osmotic regulation of *Tanypus nubifer*, *Chironomus plumosus* and *Enallagma clausum* in various concentrations of saline lake water. Physiology and Zoology 42:381–387.

LEE, T. M., AND M. K. MCCLINTOCK. 1986. Female rats in a laboratory display seasonal variation in fecundity. Journal of Reproduction and Fertility 77:51–59.

LEUCHS, H. 1986. The ventilation activity of *Chironomus* larvae (Diptera) from shallow and deep lakes and the resulting water circulation in correlation to temperature and oxygen conditions. Archiv für Hydrobiologie 108: 281–299.

LEWANDOWSKI, J., AND M. HUPFER. 2005. Effect of macrozoobenthos on two-dimensional small-scale heterogeneity of pore water phosphorus concentrations in lake sediments: a laboratory study. Limnology and Oceanography 50:1106–1118.

MARTIN, W. R., AND F. L. SAYLES. 1987. Seasonal cycles of particle and solute transport processes in nearshore sediments: $^{222}Rn/^{226}Ra$ and $^{234}Th/^{238}U$ disequilibrium at a site in Buzzards Bay, MA. Geochimica et Cosmochimica Acta 51:927–943.

MCLACHLAN, A. J. 1977. Some effects of tube shape on the feeding of *Chironomus plumosus* L. (Diptera: Chironomidae). Journal of Animal Ecology 46:139–146.

MCLACHLAN, A. J., AND M. A. CANTRELL. 1976. Sediment development and its influence on the distribution and tube structure of *Chironomus plumosus* L. (Chironomidae, Diptera) in a new impoundment. Freshwater Biology 6:437–443.

MEYSMAN, F. J. R., O. S. GALAKTIONOV, B. GRIBSHOLT, AND J. J. MIDDELBURG. 2006a. Bioirrigation in permeable sediments: advective pore-water transport induced by burrow ventilation. Limnology and Oceanography 51: 142–156.

MEYSMAN, F. J. R., O. S. GALAKTIONOV, B. GRIBSHOLT, AND J. J. MIDDELBURG. 2006b. Bio-irrigation in permeable sediments: an assessment of model complexity. Journal of Marine Research 64:589–627.

MUTZ, M., E. KALBUS, AND S. MEINECKE. 2007. Effect of instream wood on vertical water flux in low-energy sand bed flume experiments. Water Resources Research 43:1–10.

NAGELL, B., AND C. C. LANDAHL. 1978. Resistance to anoxia of *Chironomus plumosus* and *Chironomus anthracinus* (Diptera) larvae. Holarctic Ecology 1:333–336.

NAYLOR, E. 1963. Temperature relationships of the locomotor rhythm of *Carcinus*. Journal of Experimental Biology 40: 669–679.

NEUMANN, D. 1965. Photoperiodische Steuerung der 15-tagigen lunaren Metamorphose-Periodik von *Clunio* Population (Diptera: Chironomidae). Zeitschrift für Naturforschung 206:818–819.

NIELSEN, J. S., N. T. ERIKSEN, J. J. L. IVERSEN, AND H. U. RIISGÅRD. 1995. Feeding, growth and respiration in the polychaetes *Nereis diversicolor* (facultative filter-feeder) and *N. virens* (omnivorous) – a comparative study. Marine Ecology Progress Series 125:149–158.

OSOVITZ, C. J., AND D. JULIAN. 2002. Burrow irrigation behaviour of *Urechis caupo*, a filter-feeding marine invertebrate, in its natural habitat. Marine Ecology Progress Series 245:149–155.

PINDER, L. 1986. Biology of freshwater Chironomidae. Annual Review of Entomology 31:1–23.

PLATZER, I. 1967. Untersuchungen zur Temperaturadaption der tropischen Chironomidenart *Chironomus strenskei* Fittkau (Diptera). Zeitschrift für vergleichende Physiologie 54:58–74.

POLERECKY, L., N. VOLKENBORN, AND P. STIEF. 2006. High temporal resolution oxygen imaging in bioirrigated sediments. Environmental Science and Technology 40: 5763–5769.

REVSBECH, N. P., L. P. NIELSEN, AND N. B. RAMSING. 1998. A novel microsensor for determination of apparent diffusivity in sediments. Limnology and Oceanography 43: 986–992.

RIISGÅRD, H. U., AND P. S. LARSEN. 2005. Water pumping and analysis of flow in burrowing zoobenthos: an overview. Aquatic Ecology 39:237–258.

RIISGÅRD, H. U., A. VEDEL, H. BOYE, AND P. S. LARSEN. 1992. Filter-net structure and pumping activity in the polychaete *Nereis diversicolor*: effects of temperature and pump-modelling. Marine Ecology Progress Series 83: 79–89.

ROSKOSCH, A. 2011. The influence of macrozoobenthos in lake sediments on hydrodynamic transport processes and

biogeochemical impacts. PhD Dissertation, Leibnitz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany.

ROSKOSCH, A., M. HUPFER, G. NÜTZMANN, AND J. LEWANDOWSKI. 2011. Measurement techniques for quantification of pumping activity of invertebrates in small burrows. Fundamental and Applied Limnology 17:89–110.

ROSKOSCH, A., M. R. MORAD, A. KHALILI, AND J. LEWANDOWSKI. 2010. Bioirrigation by *Chironomus plumosus*: advective flow investigated by particle image velocimetry. Journal of the North American Benthological Society 29: 789–802.

SAUNDERS, D. S., R. D. LEWIS, AND G. R. WARMAN. 2004. Photoperiodic induction of diapause: opening the black box. Physiological Entomology 29:1–15.

SCHLÜTER, M., E. SAUTER, H.-P. HANSEN, AND E. SUESS. 2000. Seasonal variations of bioirrigation in coastal sediments: modelling of field data. Geochimica et Cosmochimica Acta 64:821–834.

SEYMOUR, M. K. 1972. Effects of temperature change on irrigation rate in *Arenicola marina* (L.). Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology 43:553–564.

SMETHIE, W. M., C. A. NITTROUER, AND R. F. L. SELF. 2003. The use of radon-222 as a tracer of sediment irrigation and mixing on the Washington continental shelf. Marine Geology 42:173–200.

STIEF, P., D. ALTMANN, D. DE BEER, R. BIEG, AND A. KURECK. 2004. Microbial activities in the burrow environment of the potamal mayfly *Ephoron virgo*. Freshwater Biology 49:1152–1163.

STIEF, P., AND D. DE BEER. 2006. Probing the microenvironment of freshwater sediment macrofauna: implications of deposit-feeding and bioirrigation for nitrogen cycling. Limnology and Oceanography 51:2538–2548.

STIEF, P., AND A. SCHRAMM. 2010. Regulation of nitrous oxide emission associated with benthic invertebrates. Freshwater Biology 55:1647–1657.

SVENSSON, J. M., AND L. LEONARDSON. 1996. Effects of bioturbation by tube-dwelling chironomid larvae on oxygen uptake and denitrification in eutrophic lake sediments. Freshwater Biology 35:289–300.

VAN DIJK, P. L. M., I. HARDEWIG, AND F. HÖLKER. 2005. Energy reserves during food deprivation and compensatory growth in juvenile roach: the importance of season and temperature. Journal of Fish Biology 66:167–181.

WALSHE, B. M. 1948. The oxygen requirements and thermal resistance of chironomid larvae from flowing and from still waters. Journal of Experimental Biology 25:35–44.

WALSHE, B. M. 1950. The function of haemoglobin in *Chironomus plumosus* under natural conditions. Journal of Experimental Biology 27:73–95.

WALSHE, B. M. 1951. The function of haemoglobin in relation to filter feeding in leaf-mining chironomid larvae. Journal of Experimental Biology 28:57–61.

WANG, Y., AND P. VAN CAPPELLEN. 1996. A multicomponent reactive transport model of early diagenesis: application to redox cycling in coastal marine sediments. Geochimica et Cosmochimica Acta 60:2993–3014.

WILHELM, S., AND R. ADRIAN. 2008. Impact of summer warming on the thermal characteristics of a polymictic lake and consequences for oxygen, nutrients and phytoplankton. Freshwater Biology 53:226–237.

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