The Chaoborus pump: Migrating phantom midge larvae sustain hypolimnetic oxygen deficiency and nutrient internal loading in lakes

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Abstract

Hypolimnetic oxygen demand in lakes is often assumed to be driven mainly by sediment microbial processes, while the role of Chaoborus larvae, which are prevalent in eutrophic lakes with hypoxic to anoxic bottoms, has been overlooked. We experimentally measured the respiration rates of C. flavicans at different temperatures yielding a Q10 of 1.44 ± 1.71 and a respiratory quotient of 0.84 ± 0.98. Applying the experimental data in a system analytical approach, we showed that migrating Chaoborus larvae can significantly add to the water column and sediment oxygen demand, and contribute to the observed linear relationship between water column respiration and depth. The estimated phosphorus excretion by Chaoborus in sediment is comparable in magnitude to the required phosphorus loading for eutrophication. Migrating Chaoborus larvae thereby essentially trap nutrients between the water column and the sediment, and this continuous internal loading of nutrients would delay lake remediation even when external inputs are stopped.

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1. Introduction

The evolution of oxygenic photosynthesis in Earth's history drove the emergence of aerobic metabolism (Koop et al., 2005; Allen and Martin, 2007) and the marginalization of free-living anaerobes to fringe hypoxic/anoxic habitats (Hedges et al., 2004; Schirrmeister et al., 2013). The range expansion of aerobic life forms continued until the recent centuries when anthropogenic eutrophication has caused deoxygenation of coastal and inland waters (Smith, 2003). This is reflected in lake sediment records of animal remains, most notably those of chironomids and Chaoborus spp., both of which are tolerant of low oxygen condition (Quinlan and Smol, 2001, 2010). Chaoborus spp., in particular, are highly prevalent in eutrophic and dystrophic lakes (Gosselin and Hare, 2003; Luoto and Nevalainen, 2009). Chironomid head capsules and Chaoborus mandibles are well preserved in sediments, and are therefore useful palaeolimnological indicators of major shifts in lake trophic state (Sweetman and Smol, 2006; Quinlan and Smol, 2010).

Lake remediation strategies often revolve around nutrient reduction and artificial aeration but with questionable results (Schindler, 2006; Singleton and Little, 2006; Conley et al., 2009). Internal nutrient loading can continue for years even after reduction of external input and artificial aeration, although the underlying reasons are not fully understood (Gächter and Wehrli, 1998; Hupfer and Lewandowski, 2008). Over the past four decades, researchers have considered several factors to explain or predict hypolimnetic oxygen demand, most commonly Secchi depth, chlorophyll, productivity, temperature, external loading, total phosphorus, reduced substrates from sediment, and sediment oxygen demand (Table S1). These studies, however, do not explain the oft-reported positive relationship between areal hypolimnetic oxygen demand and hypolimnion thickness (Charlton, 1980; Müller et al., 2012), and rarely consider oxygen draw-down by meiofauna. Soster et al. (2015) suggested that bioirrigation by chironomid larvae could stimulate microbial oxygen demand in the burrows, leading to an increased hypolimnetic oxygen deficit.

Unlike the permanently benthic chironomid larvae, Chaoborus...
migrate diurnally and, therefore, influence the sediment and water column chemistry on a twice daily basis. A recent study suggests that habitat expansion and proliferation of Chaoborus are intricately linked to deoxygenation and methanogenesis in lake sediments, and which may represent the tipping point in lake ecosystem structure where successful invasion by Chaoborus would accelerate and sustain deterioration of water quality (McGinnis et al., 2017). To our knowledge, Chaoborus are the only significant bioturbators in lake sediments with anoxic bottom waters, and their presence could control not only oxygen dynamics but also nutrient fluxes across the sediment-water interface (Gosselin and Hare, 2003). The influence of Chaoborus, however, has long been overlooked in lake remediation and management. In this study, we measured the vertical migration speed and respiration rate of Chaoborus larvae, and applied the data in a system analytical approach to examine their roles in driving oxygen and nutrient dynamics in a lake-wide context. Our results suggest that Chaoborus activities could account for a significant but hitherto overlooked portion of both the hypolimnetic and sediment oxygen demands, and internal nutrient loading.

2. Material and methods

2.1. In situ measurement of Chaoborus migration

Chaoborus migration was monitored using a 5-beam acoustic Doppler current profiler (ADCP; Teledyne RDV50, 492 kHz) in Lake Soppensee, Switzerland, a eutrophic lake with a long history of anoxic bottom water (Gruber et al., 2000). The ADCP was bottom mounted (upward looking) in 20 m water depth and mounted to a gimballed frame. The ADCP recorded backscatter with a 0.5 m resolution from ca. 2.5 m from the sediment floor to within 1 m of the surface. The ADCP backscatter is an excellent method to track Chaoborus movement because of the strong signal resulting from their gas vesicles (Lorke et al., 2004). In situ larvae abundance was estimated from night-time vertical plankton net tows (500 μm mesh, 0.25 m opening).

2.2. Laboratory measurements of Chaoborus respiration

Respiration rates of Chaoborus flavicans larvae (instar 3–4) were measured both in terms of CO2 production and O2 consumption. The larvae were collected from Lake Dagow, Germany by night-time surface net tows, sorted into bottles with 20 μm-filtered lake water. The larvae were then transferred to a 365-ml round-bottom flask with 130 ml of filtered lake water. The flask was connected via a closed circuit to a Los-Gatos CO2 analyser, which measured CO2 concentration in the headspace continuously (McGinnis et al., 2017). The water was slowly stirred by a magnetic stirrer (speed ~30 rpm) to equilibrate the gases between the aqueous phase and the head space. Respiration rate in terms of CO2 production was calculated based on linear increase in headspace CO2 over time. The experiments were done at ca. 20 and 8 °C with only 99–100 larvae. A bottle with only filtered lake water was used as the control.

3. Results and discussion

3.1. Diurnal migration of Chaoborus larvae

Diurnal migration of Chaoborus larvae in the eutrophic Lake Soppensee (ca. 26 m deep), Switzerland was observed by ADCP (Fig. 1) similar to the work by Lorke et al. (2004). Dense biomass of Chaoborus larvae could be visualised on the sonogram migrating from the lake bottom up to near the surface at night, and returned to the bottom during the day; the corresponding swimming speed (ascent and descent) was estimated to be ca. 310 m d\(^{-1}\). This was comparable to rates reported by Lorke et al. (2004) and McGinnis et al. (2017). From the net tow samples, the in situ abundances of instars 3 and 4 were measured at ca. 17,000 ind m\(^{-2}\) (S.E. = 2523). Instars 1 and 2 were not counted because the large mesh size tended to under-sample the smaller life stages. Assuming the younger instars accounted for half of the in situ populations, the total larvae abundance would be ca. 34,000 ind m\(^{-2}\). In subsequent analysis of respiration and nutrient transport, we considered only instar 3–4.

3.2. Respiration of Chaoborus larvae

Respiration rates of Chaoborus flavicans larvae (instars 3–4) in terms of CO2 production were consistent across trials, averaging 1.87 and 1.10 μmol ind \(^{-1}\) d\(^{-1}\) at 23.0 and 8.4 °C, respectively. O2 consumption rate was 2.21 and 1.12 μmol ind \(^{-1}\) d\(^{-1}\) at 20.7 and 8.4 °C, respectively (Table S2). The corresponding Q10 was 1.44 for CO2 production and 1.71 for O2 consumption, both lower than the usually assumed value of 2–3, but close to the measured Q10 for nutrient excretions by Chaoborus (1.49–1.66) (Fukuhara and Yasuda, 1985, 1989). This suggests that Chaoborus metabolism is less sensitive to temperature change than expected as the larvae routinely migrate between the cold lake bottom and the warm upper water. The derived respiratory quotient was 0.84 and 0.98 for the high and low temperature, respectively. The values are similar to that reported for C. punctipennis (Ransom et al., 1969) and are indicative of a protein-rich diet for this predatory species.

To put these respiration rates in an ecological context, we considered a C. flavicans population density of 4000–100,000 ind m\(^{-2}\) commonly found in nature (Gosselin and Hare, 2003). Of these, we assumed half are non-migrating instars 1 and 2, and half are instars 3 and 4 migrating diurnally across the hypolimnion (8 °C). Using a swimming speed of 310 m d\(^{-1}\) estimated from the
ADCP data, we calculated the time spent by instar 3–4 travelling through the water column as a function of hypolimnion thickness; we further assumed they spend half of the non-migrating time in the hypolimnion. From this we calculated the daily water column respiration \( R_w \; (\text{gO}_2 \text{m}^{-2} \text{d}^{-1}) \) by instar 3–4 as:

\[
R_w = \frac{rN}{2} \left( \frac{2H}{S} + 1 \right)
\]

where \( r \) and \( N \) are respectively the individual respiration rate \( (\text{gO}_2 \text{ind}^{-1} \text{d}^{-1}) \) and abundance \( (\text{ind} \text{m}^{-2}) \), \( H \) is hypolimnion thickness \( (\text{m}) \), and \( S \) is swimming speed \( (\text{m} \text{d}^{-1}) \). We compared the results against published water column respiration for eutrophic lakes (Müller et al., 2012) (Fig. 2). Even at a modest population density \( (20,000 \text{ind} \text{m}^{-2} \text{of instar 3–4}) \), Chaoborus respiration was equivalent to 32–63% of the total observed hypolimnetic respiration for depth 5–40 m. At higher density \( (50,000 \text{ind} \text{m}^{-2}) \), Chaoborus respiration could theoretically exceed the observed oxygen consumption rate in shallow lakes, and could account for 24% of the observed linear relationship between hypolimnetic respiration and depth. Besides microbes, Chaoborus therefore constitute an important but overlooked hypolimnetic oxygen sink, especially in shallow lakes and at high population densities. Some Chaoborus populations have a life-span extending into the ice-covered periods in temperate lakes (Eaton, 1983; Liljendahl-Nurminen et al., 2002; our own observations), during which time oxygen production and infusion to the water column would be very limited, and the oxygen deficit created by Chaoborus could be even more severe. By depleting the water column of oxygen, Chaoborus significantly influence the carbon and energy balance of the system, and engineer a hypoxic/anoxic environment in which they can thrive.

3.3. Influence of Chaoborus on sediment oxygen demand

Migrating zooplankton are known to mediate vertical transport of materials throughout the water column, commonly described as the ‘biological pump’ (Dam et al., 1995; Steinberg et al., 2000). Chaoborus larvae are unique in the sense that they are often the only organisms that migrate directly into the lake sediment. This ‘Chaoborus pump’ can therefore strongly affect sediment biogeochemistry in ways few other diurnal migrants can. Assuming instars 3 and 4 spend half of the non-migrating time in the sediment (the other half feeding in the water column), we used our respiration data at 8 °C to estimate the amount of respired CO2 added to the sediment as \( rN[1-(2H/S)]/2 \) (Fig. 3a). Similarly, we also calculated O2 uptake by Chaoborus in the sediment (Fig. 3b).

Gudasz et al. (2010) summarized sediment remineralization rates across many temperate lakes, which were ca. 100 mgC m\(^{-2} \text{d}^{-1} \) at 8 °C. Assuming equimolar C to O2 conversion, this translates to a potential sediment oxygen demand (SOD) of 0.27 gO2 m\(^{-2} \text{d}^{-1} \) (range 0.07–0.67). Our estimated Chaoborus driven potential SOD was equivalent to an average of 10 to >100% total SOD (Fig. 3b). We described this as potential SOD because the larvae are usually found in anoxic bottom, and under anoxia they are capable of anaerobic respiration (Ransom et al., 1969). Nevertheless, our experiments and calculations suggest that in eutrophic lake sediments where Chaoborus larvae are abundant, respiration by the larvae could add a considerable amount of sediment oxygen demand not accounted for in routine sediment remineralization measurements, and help maintain the oxygen tension in the benthos.

3.4. Influence of Chaoborus on sediment methane outflux

Chaoborus larvae have the unique adaptation of utilizing sediment methane to inflate their gas sacs and gain buoyancy advantage for migration (McGinnis et al., 2017). This process also facilitates the transport of sediment methane to shallower water during migration. McGinnis et al. (2017) estimated that at a density of 2000–130,000 ind \text{m}^{-2}, the migration-driven upward methane flux is 10–2000 mmol \text{m}^{-2} \text{yr}^{-1}, which can surpass diffusive transport across the sediment-water interface. It is worth noting that the calculated CO2 addition to the sediment due to Chaoborus respiration was higher than, but on the same order of magnitude as, the methane outflux calculated by McGinnis et al. (2017). If we also consider bioturbation effects by Chaoborus within the sediment (Gosselin and Hare, 2003), which would increase methane bubble outflux (Bezerra-Neto et al., 2012), the two values (CO2 addition vs. CH4 export) should approach one another. Putting this in an ecosystem context, migrating Chaoborus larvae can be seen as driving an apparent CO2-to-CH4 exchange in the sediment. Because CH4 has a ca. 28 times the global warming potential as CO2 (IPCC, 2013), this gaseous exchange due to migrating Chaoborus larvae could accelerate the overall warming contribution by eutrophic lakes.

3.5. Influence of Chaoborus on nutrient transport

During the eutrophication history, organic and nutrient input turns the sediment and bottom water increasingly anoxic and fundamentally changes the benthic environment. In the literature, particle sedimentation is often assumed to be the primary input into the sediment (Grossart and Simon, 1998; Müller et al., 2012). Detrital aggregates, or ‘lake snow’, has a sinking rate of <130 m d\(^{-1} \) (Grossart and Simon, 1993), whereas Chaoborus larvae swimming speed is ca. 3 times faster (Lorke et al., 2004; McGinnis et al., 2017; this study). Therefore, migrating Chaoborus larvae can speed up chemical fluxes into the sediment by many times over particle sedimentation. Below we use an example to illustrate how this may affect lake eutrophication.

Chaoborus larvae take in organic nitrogen and phosphorus by feeding in the upper water column at night, and continue to excrete inorganic nitrogen and phosphorus when they return to the sediment during the day. The overall effect is translocation of N and P.
Fig. 3. Effects of migrating Chaoborus larvae on sediment chemistry. (a) Carbon addition to sediment by respiration; (b) Potential sediment oxygen demand by respiration; (c) Nitrogen excretion in sediment; (d) Phosphorus excretion in sediment. Chaoborus population densities (instar 3–4) represented by the different lines are shown in panel (a).

Fig. 4. Conceptual diagram of the Chaoborus pump and nutrient trap. Chaoborus larvae consume organic nutrients in the upper water and transport them to the sediment via diurnal migration, and continue to excrete nutrients while residing in the sediment. Oxygen deficit in the sediment partly created by Chaoborus respiration keeps the nutrients in dissolved (reduced) forms that readily diffuse back to the overlying water. The predation-migration-excretion of Chaoborus essentially traps the nutrients and sustains nutrient internal loading within the water column.
from the surface water to the sediment by burrowing *Chaoborus*. Using the larvae's length measurements (mean 11.43 mm), we estimated their dry mass (*Dumont and Balvay, 1979*), and converted that to temperature specific excretion rates based on published algorithms (*Devine and Vanni, 2002*) to arrive at the excretion rates of 0.021 μmol N ind⁻¹ d⁻¹ and 0.11 μmol P ind⁻¹ d⁻¹. We then calculated N and P fluxes into the sediment mediated by migrating *Chaoborus* larvae as a function of population density and water depth (i.e. time spent in the sediment) (Fig. 3c and d).

External phosphorus loading is considered to be the main driving force of lake eutrophication, and a loading of ca. 0.2 g m⁻² yr⁻¹ is expected to result in a mesotrophic state, ca. 0.3 g m⁻² yr⁻¹ for eutrophic, and ca. 0.4 g m⁻² yr⁻¹ for hypertrophic (*Shannon and Brezonik, 1972*). Given that *Chaoborus* larvae are common in mesotrophic to hypertrophic waters, we ask whether migrating *Chaoborus* larvae would facilitate translocation of surface P loading to the bottom sediment. Using the estimated P excretion rate, we calculated the annual P flux into sediment by burrowing *Chaoborus* as a function of depth and *Chaoborus* abundance (Table S3). The estimated value ranged from 0.07 to 3.09 g m⁻³ as a function of depth and Chaoborus

**Figure 4.** The nutrients are therefore essentially trapped by sediment, and reduction of external input will not lead to immediate improvement because of this continuous recycling (internal loading) of nutrients.

4. Conclusions

Conventional studies assume that deoxygenation of eutrophic lake waters is driven primarily by internal oxygen consumption by microbes. Lake management and restoration by nutrient reduction and artificial aeration often fail to produce the desired outcome. Using a system analytical approach with experimental data, we revealed novel aspects of *Chaoborus* in driving ecosystem functioning in lakes and reservoirs. *Chaoborus* larvae seem to account for a significant fraction of both the hypolimnetic and sediment oxygen demands, and effectively trap nutrients between the water and the sediment, where they will enhance the internal nutrient loading. Consequently, once *Chaoborus* larvae have successfully established their populations, they tend to maintain the status quo of eutrophic lakes and counteract lake remediation efforts. We therefore propose that to improve lake management and remediation strategies, it will require measures not only to curb external nutrient input, but also to control or reduce *Chaoborus* populations.

**Author contributions**

All authors conceived the study and collected the data; KWT and DFM analysed the data; KWT wrote the manuscript with input from all co-authors.

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**Appendix A. Supplementary data**

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.watres.2017.05.058.

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