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3   **The *Chaoborus* pump: Migrating phantom midge larvae sustain hypolimnetic oxygen**

4   **deficiency and nutrient internal loading in lakes**

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19   **Author contributions:** All authors conceived the study and collected the data; KWT and DFM

20   analysed the data; KWT wrote the manuscript with input from all co-authors.

21   **Abstract**

22   Hypolimnetic oxygen demand in lakes is often assumed to be driven mainly by sediment

23   microbial processes, while the role of *Chaoborus* larvae, which are prevalent in eutrophic

24   lakes with hypoxic to anoxic bottoms, has been overlooked. We experimentally measured

25   the respiration rates of *C. flavicans* at different temperatures yielding a Q_{10} of 1.44−1.71 and

26   a respiratory quotient of 0.84−0.98. Applying the experimental data in a system analytical

27   approach, we showed that migrating *Chaoborus* larvae can significantly add to the water

28   column and sediment oxygen demand, and contribute to the observed linear relationship

29   between water column respiration and depth. The estimated phosphorus excretion by

30   *Chaoborus* in sediment is comparable in magnitude to the required phosphorus loading for

31   eutrophication. Migrating *Chaoborus* larvae thereby essentially trap nutrients between the

32   water column and the sediment, and this continuous internal loading of nutrients would

33   delay lake remediation even when external inputs are stopped.

34

35   **Keywords:** *Chaoborus*; eutrophication; oxygen; nutrient; remediation

1. Introduction

The evolvement of oxygenic photosynthesis in Earth's history drove the emergence of aerobic metabolism (Kopp 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 et al., 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.,

59   2012), and rarely consider oxygen draw-down by meiofauna. Soster et al. (2015) suggested

60   that bioirrigation by chironomid larvae could stimulate microbial oxygen demand in the

61   burrows, leading to an increased hypolimnetic oxygen deficit.

62   Unlike the permanently benthic chironomid larvae, *Chaoborus* migrate diurnally and,

63   therefore, influence the sediment and water column chemistry on a twice daily basis. A

64   recent study suggests that habitat expansion and proliferation of *Chaoborus* are intricately

65   linked to deoxygenation and methanogenesis in lake sediments, and which may represent

66   the tipping point in lake ecosystem structure where successful invasion by *Chaoborus* would

67   accelerate and sustain deterioration of water quality (McGinnis et al., 2017). To our

68   knowledge, *Chaoborus* are the only significant bioturbators in lake sediments with anoxic

69   bottom waters, and their presence could control not only oxygen dynamics but also nutrient

70   fluxes across the sediment-water interface (Gosselin and Hare, 2003). The influence of

71   *Chaoborus*, however, has long been overlooked in lake remediation and management. In

72   this study, we measured the vertical migration speed and respiration rate of *Chaoborus*

73   larvae, and applied the data in a system analytical approach to examine their roles in driving

74   oxygen and nutrient dynamics in a lake-wide context. Our results suggest that *Chaoborus*

75   activities could account for a significant but hitherto overlooked portion of both the

76   hypolimnetic and sediment oxygen demands, and internal nutrient loading.

77

78   **2. Material and methods**

79   *2.1. In situ* measurement of *Chaoborus* migration

80   *Chaoborus* migration was monitored using a 5-beam acoustic Doppler current

81   profiler (ADCP; Teledyne RDI V50, 492 kHz) in Lake Soppensee, Switzerland, a eutrophic lake

82   with a long history of anoxic bottom water (Gruber et al., 2000). The ADCP was bottom

83   mounted (upward looking) in 20 m water depth and mounted to a gimballed frame. The

84   ADCP recorded backscatter with a 0.5 m resolution from ca. 2.5 m from the sediment floor

85   to within 1 m of the surface. The ADCP backscatter is an excellent method to track

86   *Chaoborus* movement because of the strong signal resulting from their gas vesicles (Lorke et

87   al., 2004). In situ larvae abundance was estimated from night-time vertical plankton net

88   tows (500 μm mesh, 0.25 m opening).

89

90   *2.2. Laboratory measurements of* Chaoborus *respiration*

91   Respiration rates of *Chaoborus flavicans* larvae (instar 3−4) were measured both in

92   terms of CO_2 production and O_2 consumption. The larvae were collected from Lake Dagow,

93   Germany by night-time surface net tows, sorted into bottles with 20 μm-filtered lake water,

94   and fed natural zooplankton assemblage overnight. Before each experiment, the larvae

95   were rinsed 3 times in filtered lake water to remove detritus and food particles, and then

96   transferred to a 365-ml round-bottom flask with 130 ml of filtered lake water. The flask was

97   connected via a closed circuit to a Los-Gatos CO_2 analyser, which measured CO_2

98   concentration in the headspace continuously (McGinnis et al., 2017). The water was slowly

99   stirred by a magnetic stirrer (speed <30 rpm) to equilibrate the gases between the aqueous

100   phase and the head space. Respiration rate in terms of CO_2 production was calculated based

101   on linear increase in headspace CO_2 over time. The experiments were done at ca. 20 and 8

102 °C with different numbers (17–70 total) of larvae. Water temperatures were monitored by a

103 thermometer. A flask with only filtered lake water was used as the control.

104 O_2 consumption was measured in a separate series of experiments in which the

105 larvae were placed in a 365-ml BOD bottle filled with filtered lake water (no head space). A

106 glass-fibre O_2 probe was inserted through the stopper into the water; the probe was

107 connected to a Presense Firesting O_2 meter. Respiration rate in terms of O_2 consumption

108 was calculated based on linear decrease in dissolved O_2 over time. The experiments were

109 done at ca. 20 and 8 °C with 99–100 larvae. A bottle with only filtered lake water was used

110 as the control.

111

112 **3. Results and discussion**

113 *3.1. Diurnal migration of* Chaoborus *larvae*

114 Diurnal migration of *Chaoborus* larvae in the eutrophic Lake Soppensee (ca. 26 m deep),

115 Switzerland was observed by ADCP (Fig. 1) similar to the work by Lorke et al. (2004). Dense

116 biomass of *Chaoborus* larvae could be visualised on the sonogram migrating from the lake

117 bottom up to near the surface at night, and returned to the bottom during the day; the

118 corresponding swimming speed (ascent and descent) was estimated to be ca. 310 m d^{-1}. This

119 was comparable to rates reported by Lorke et al. (2004) and McGinnis et al. (2017). From

120 the net tow samples, the *in situ* abundances of instars 3 and 4 were measured at ca. 17,000

121 ind m^{-2} (S.E. = 2,523). Instars 1 and 2 were not counted because the large mesh size tended

122 to under-sample the smaller life stages. Assuming the younger instars accounted for half of

123   the *in situ* populations, the total larvae abundance would be ca. 34,000 ind m^{-2}. In

124   subsequent analysis of respiration and nutrient transport, we considered only instar 3-4.

125   *3.2. Respiration of* Chaoborus *larvae*

126   Respiration rates of *Chaoborus flavicans* larvae (instars 3−4) in terms of CO_2

127   production were consistent across trials, averaging 1.87 and 1.10 µmol ind^{-1} d^{-1} at 23.0 and

128   8.4 °C, respectively. O_2 consumption rate was 2.21 and 1.12 µmol ind^{-1} d^{-1} at 20.7 and 8.4 °C,

129   respectively (Table S2). The corresponding Q_{10} was 1.44 for CO_2 production and 1.71 for O_2

130   consumption, both lower than the usually assumed value of 2−3, but close to the measured

131   Q_{10} for nutrient excretions by *Chaoborus* (1.49−1.66) (Fukuhara and Yasuda, 1985; 1989).

132   This suggests that *Chaoborus* metabolism is less sensitive to temperature change than

133   expected as the larvae routinely migrate between the cold lake bottom and the warm upper

134   water. The derived respiratory quotient was 0.84 and 0.98 for the high and low

135   temperature, respectively. The values are similar to that reported for *C. punctipennis*

136   (Ransom et al., 1969) and are indicative of a protein-rich diet for this predatory species.

137   To put these respiration rates in an ecological context, we considered a *C. flavicans*

138   population density of 4,000−100,000 ind m^{-2} commonly found in nature (Gosselin and Hare,

139   2003). Of these, we assumed half are non-migrating instars 1 and 2, and half are instars 3

140   and 4 migrating diurnally across the hypolimnion (8°C). Using a swimming speed of 310 m d^{-}

141   ^{1} estimated from the ADCP data, we calculated the time spent by instar 3-4 travelling

142   through the water column as a function of hypolimnion thickness; we further assumed they

143   spend half of the non-migrating time in the hypolimnion. From this we calculated the daily

144   water column respiration (R_w; gO$_2$ m^{-2} d^{-1}) by instar 3-4 as:

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

145   where r and N are respectively the individual respiration rate (gO_2 ind^{-1} d^{-1}) and abundance

146   (ind m^{-2}), H is hypolimnion thickness (m), and S is swimming speed (m d^{-1}). We compared

147   the results against published water column respiration for eutrophic lakes (Müller et al.,

148   2012) (Fig. 2). Even at a modest population density (20,000 ind m^{-2} of instar 3-4), *Chaoborus*

149   respiration was equivalent to 32–63% of the total observed hypolimnetic respiration for

150   depth 5–40 m. At higher density (50,000 ind m^{-2}), *Chaoborus* respiration could theoretically

151   exceed the observed oxygen consumption rate in shallow lakes, and could account for 24%

152   of the observed linear relationship between hypolimnetic respiration and depth. Besides

153   microbes, *Chaoborus* therefore constitute an important but overlooked hypolimnetic

154   oxygen sink, especially in shallow lakes and at high population densities. Some *Chaoborus*

155   populations have a life-span extending into the ice-covered periods in temperate lakes

156   (Eaton, 1983; Liljendahl-Nurinen et al., 2002; our own observations), during which time

157   oxygen production and infusion to the water column would be very limited, and the oxygen

158   deficit created by *Chaoborus* could be even more severe. By depleting the water column of

159   oxygen, *Chaoborus* significantly influence the carbon and energy balance of the system, and

160   engineer a hypoxic/anoxic environment in which they can thrive.

161

162   *3.3. Influence of* Chaoborus *on sediment oxygen demand*

163   Migrating zooplankton are known to mediate vertical transport of materials

164   throughout the water column, commonly described as the 'biological pump' (Dam et al.,

165   1995; Steinberg et al., 2000). *Chaoborus* larvae are unique in the sense that they are often

166   the only organisms that migrate daily into the lake sediment. This '*Chaoborus* pump' can

167   therefore strongly affect sediment biogeochemistry in ways few other diurnal migrators can.

168   Assuming instars 3 and 4 spend half of the non-migrating time in the sediment (the other

169   half feeding in the water column), we used our respiration data at 8 °C to estimate the

170   amount of respired CO_2 added to the sediment as $rN[1-(2H/S)]/2$ (Fig. 3a). Similarly, we also

171   calculated O_2 uptake by *Chaoborus* in the sediment (Fig. 3b).

172   Gudasz et al. (2010) summarized sediment remineralization rates across many

173   temperate lakes, which were ca. 100 mgC m^{-2} d^{-1} at 8 °C. Assuming equimolar C to O_2

174   conversion, this translates to a potential sediment oxygen demand (SOD) of 0.27 gO_2 m^{-2} d^{-1}

175   (range 0.07−0.67). Our estimated *Chaoborus* driven potential SOD was equivalent to an

176   average of 10 to >100% total SOD (Fig. 3b). We described this as potential SOD because the

177   larvae are usually found in anoxic bottom, and under anoxia they are capable of anaerobic

178   respiration (Ransom et al., 1969). Nevertheless, our experiments and calculations suggest

179   that in eutrophic lake sediments where *Chaoborus* larvae are abundant, respiration by the

180   larvae could add a considerable amount of sediment oxygen demand not accounted for in

181   routine sediment remineralization measurements, and help maintain the oxygen tension in

182   the benthos.

183

184   *3.4. Influence of* Chaoborus *on sediment methane outflux*

185   *Chaoborus* larvae have the unique adaptation of utilizing sediment methane to

186   inflate their gas sacs and gain buoyancy advantage for migration (McGinnis et al., 2017).

187   This process also facilitates the transport of sediment methane to shallower water during

188   migration. McGinnis et al. (2017) estimated that at a density of 2,000−130,000 ind m^{-2}, the

189 migration-driven upward methane flux is 10–2,000 mmol m^{-2} yr^{-1}, which can surpass

190 diffusive transport across the sediment-water interface. It is worth noting that the

191 calculated CO_2 addition to the sediment due to *Chaoborus* respiration was higher than, but

192 on the same order of magnitude as, the methane outflux calculated by McGinnis et al.

193 (2017). If we also consider bioturbation effects by *Chaoborus* within the sediment (Gosselin

194 and Hare, 2003), which would increase methane bubble outflux (Bezerra-Neto et al., 2012),

195 the two values (CO_2 addition vs. CH_4 export) should approach one another. Putting this in an

196 ecosystem context, migrating *Chaoborus* larvae can be seen as driving an apparent CO_2-to-

197 CH_4 exchange in the sediment. Because CH_4 has a ca. 28 times the global warming potential

198 as CO_2 (IPCC 2013), this gaseous exchange due to migrating *Chaoborus* larvae could

199 accelerate the overall warming contribution by eutrophic lakes.

200

201 *3.5. Influence of* Chaoborus *on nutrient transport*

202 During the eutrophication history, organic and nutrient input turns the sediment and

203 bottom water increasingly anoxic and fundamentally changes the benthic environment. In

204 the literature, particule sedimentation is often assumed to be the primary input into the

205 sediment (Grossart and Simon, 1998; Müller et al., 2012). Detrital aggregates, or 'lake

206 snow', has a sinking rate of ≤ 130 m d^{-1} (Grossart and Simon, 1993), whereas *Chaoborus*

207 larvae swimming speed is ca. 3 times faster (Lorke et al., 2004; McGinnis et al., 2017; this

208 study). Therefore, migrating *Chaoborus* larvae can speed up chemical fluxes into the

209 sediment by many folds over particle sedimentation. Below we use an example to illustrate

210 how this may affect lake eutrophication.

211   *Chaoborus* larvae take in organic nitrogen and phosphorus by feeding in the upper

212   water column at night, and continue to excrete inorganic nitrogen and phosphorus when

213   they return to the sediment during the day. The overall effect is translocation of N and P

214   from the surface water to the sediment by burrowing *Chaoborus*. Using the larvae's length

215   measurements (mean 11.43 mm), we estimated their dry mass (Durmont and Balvay, 1979),

216   and converted that to temperature specific excretion rates based on published algorithms

217   (Devine and Vanni, 2002) to arrive at the excretion rates of 0.021 µmol N ind^{-1} d^{-1} and 0.11

218   µmol P ind^{-1} d^{-1}. We then calculated N and P fluxes into the sediment mediated by migrating

219   *Chaoborus* larvae as a function of population density and water depth (i.e. time spent in the

220   sediment) (Fig. 3c, d).

221   External phosphorus loading is considered to be the main driving force of lake

222   eutrophication, and a loading of ca. 0.2 g m^{-2} yr^{-1} is expected to result in a mesotrophic

223   state, ca. 0.3 g m^{-2} yr^{-1} for eutrophic, and ca. 0.4 g m^{-2} yr^{-1} for hypertrophic (Shannon and

224   Brezonik, 1972). Given that *Chaoborus* larvae are common in mesotrophic to hypertrophic

225   waters, we ask whether migrating *Chaoborus* larvae would facilitate translocation of surface

226   P loading to the bottom sediment. Using the estimated P excretion rate, we calculated the

227   annual P flux into sediment by burrowing *Chaoborus* as a function of depth and *Chaoborus*

228   abundance (Table S3). The estimated value ranged from 0.07 to 3.09 g m^{-2} yr^{-1}, equivalent to

229   ca. 35−770% of external P loading across the trophic gradient. We should emphasize that

230   our calculation is not actual P sequestration because it does not account for nutrient

231   resuspension from the sediment due to bioturbation (Gosselin and Hare, 2003).

232   Nevertheless, considering that the calculated P-downward flux was on the same order of

233   magnitude or even exceeded the 'required' external P loading for eutrophication, this

234   exercise has important implications for lake ecology and management: Surface nutrient

235 loading can be largely pumped by migrating *Chaoborus* larvae into the lake bottom, where

236 the strong oxygen deficit partly created by *Chaoborus* respiration would keep the nutrients

237 in dissolved (reduced) forms that readily diffuse back to the overlying water (Fig. 4). The

238 nutrients are therefore essentially trapped by migrating *Chaoborus* larvae between the

239 water column and the sediment, and reduction of external input will not lead to immediate

240 improvement because of this continuous recycling (internal loading) of nutrients.

241 In addition to direct nutrient pumping into the sediment, *Chaoborus* may also

242 indirectly affect nutrient processes within the water column. As key planktivores, the

243 presence of *Chaoborus* often drastically alters the zooplankton abundance, species

244 composition, and size spectrum (Hanazato and Yasuno, 1989), with cascading effect through

245 the food chain (Pagano et al., 2003). The subsequent effects on nutrient recycling (e.g. via

246 excretion) and export (e.g. via aggregate and fecal pellet production) among the plankton

247 would have important ramifications for the ecosystem (Vanni, 1996).

248

249 **4. Conclusions**

250 Conventional studies assume that deoxygenation of eutrophic lake waters is driven

251 primarily by internal oxygen consumption by microbes. Lake management and restoration

252 by nutrient reduction and artificial aeration often fail to produce the desired outcome. Using

253 a system analytical approach with experimental data, we revealed novel aspects of

254 *Chaoborus* in driving ecosystem functioning in lakes and reservoirs. *Chaoborus* larvae seem

255 to account for a significant fraction of both the hypolimnetic and sediment oxygen

256 demands, and effectively trap nutrients between the water and the sediment, where they

257 will enhance the internal nutrient loading. Consequently, once *Chaoborus* larvae have

258 successfully established their populations, they tend to maintain the status quo of eutrophic

259 lakes and counteract lake remediation efforts. We therefore propose that to improve lake

260 management and remediation strategies, it will require measures not only to curb external

261 nutrient input, but also to control or reduce *Chaoborus* populations.

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380

Figure captions

Fig. 1. Sonogram of diurnally migrating *Chaoborus sp.* larvae (red band) in Lake Soppensee

(ca. 26 m deep), Switzerland based on ADCP V50 measurements over a 3-day period. The

water depth where the ADCP was deployed was 20 m.

Fig. 2. Water column oxygen consumption as a function of hypolimnion thickness. Solid

symbol and solid line are observed areal hypolimnetic mineralization (AHM) and the

corresponding linear regression based on Müller et al. (2012). Open symbols and dash lines

are water column respiration for different *Chaoborus* population densities (instar 3-4). Table

shows % AHM change (slope of the regression line) that can be explained by *Chaoborus*

respiration.

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 transports 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

403   dissolved (reduced) forms that readily diffuse back to the overlying water. The predation-

404   migration-excretion of *Chaoborus* essentially traps the nutrients and sustains nutrient

405   internal loading within the water column.
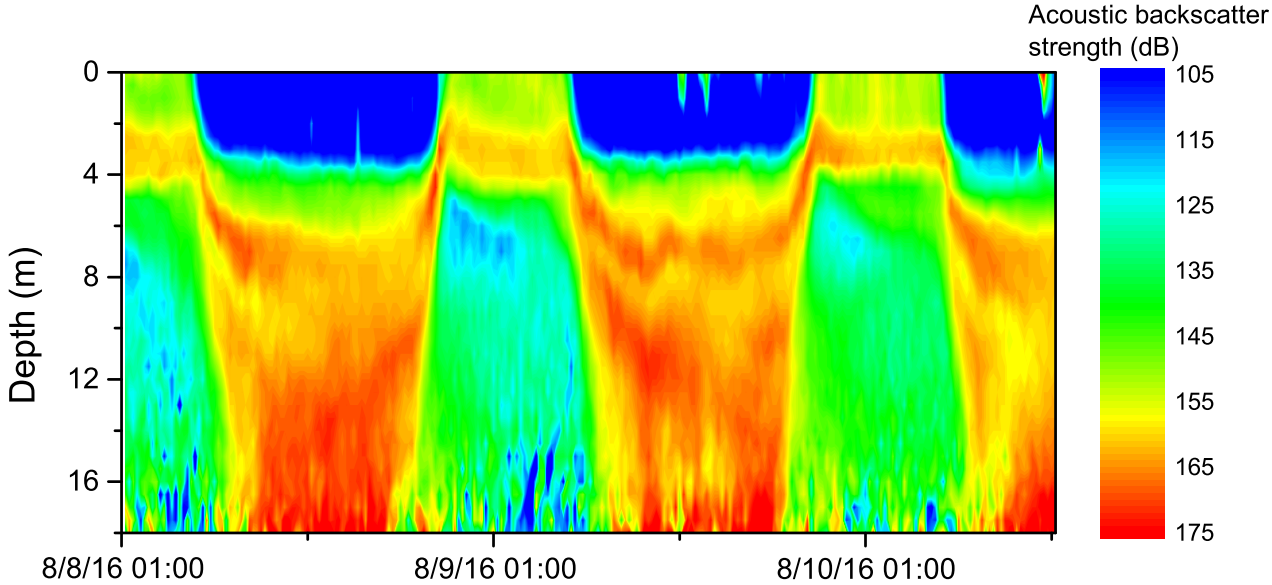
Figure 1
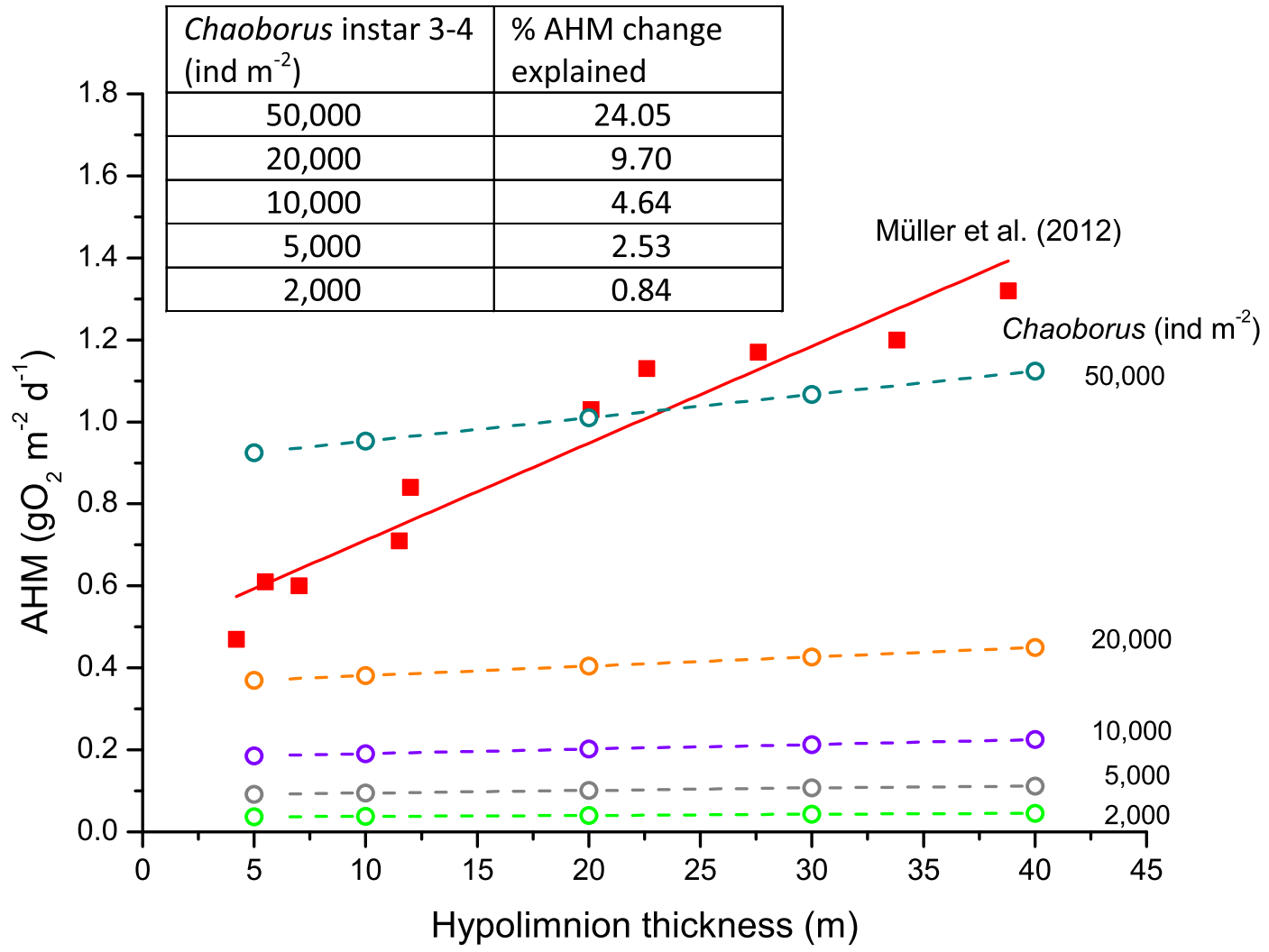
Figure 2

Figure 3

Figure 4

Predation

Excrement settling

O₂

Respiration

Diurnal migration

Dissolved nutrient release

Depth

Anoxic sediment

Nutrients
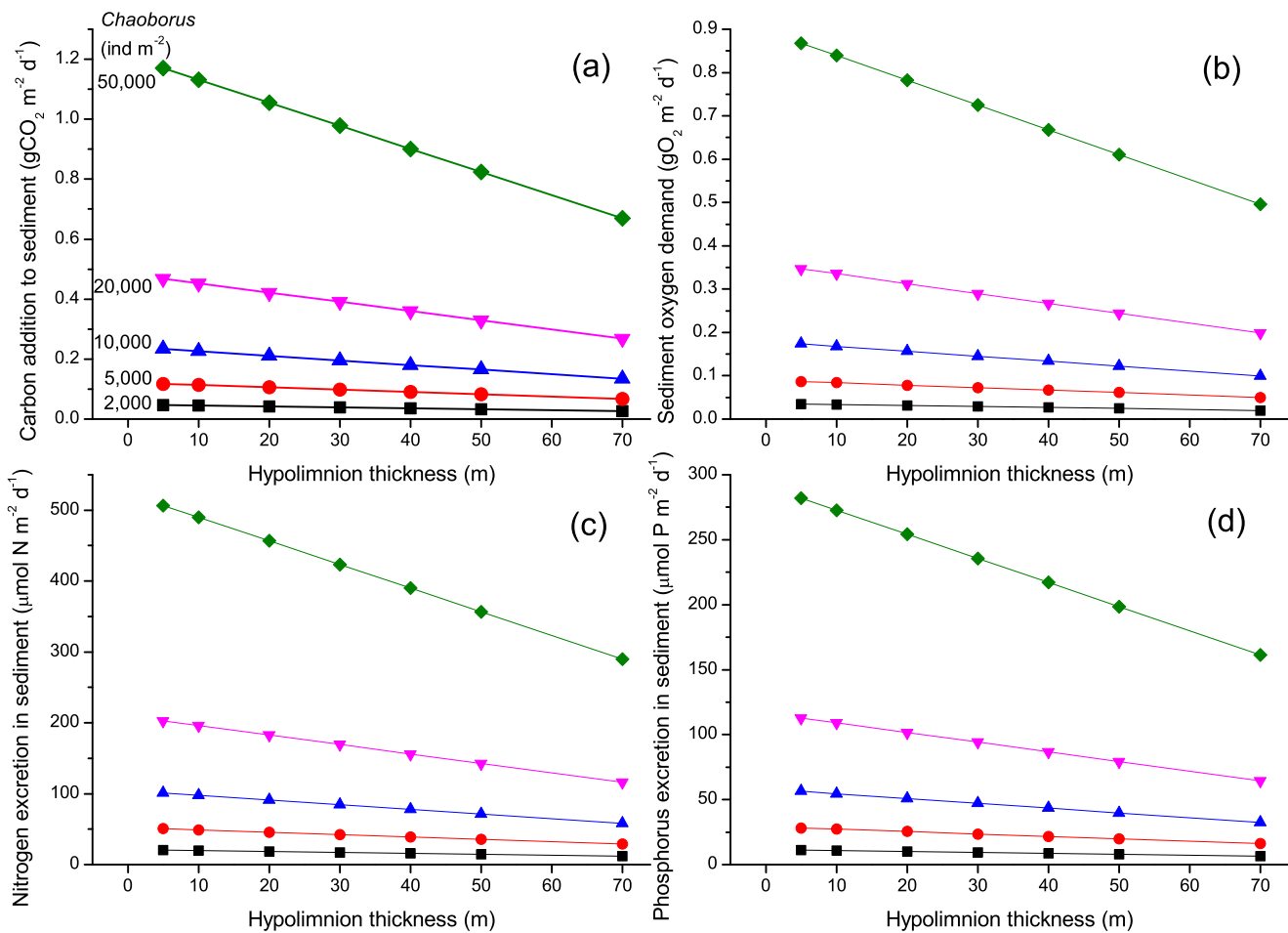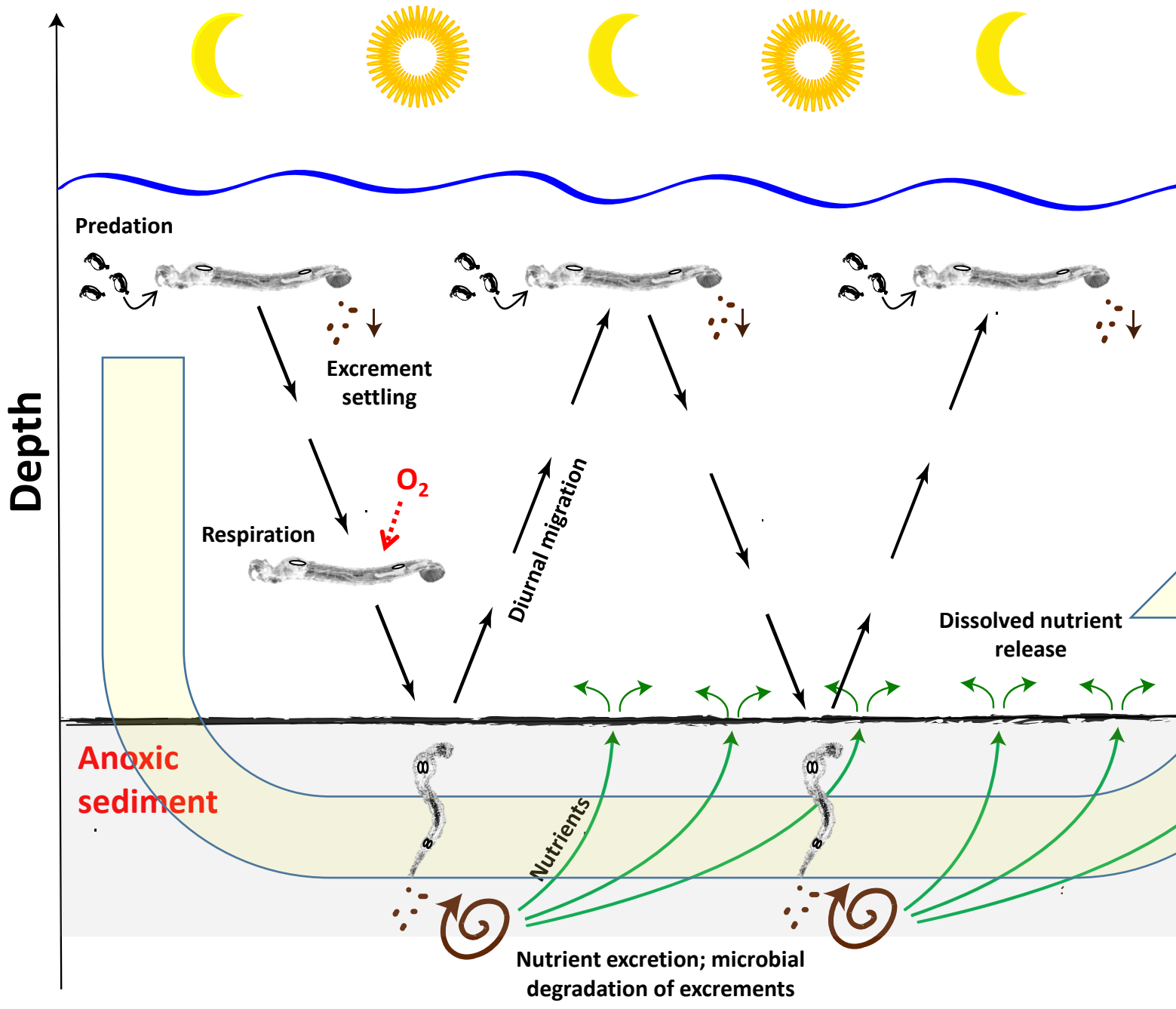
Nutrient excretion; microbial degradation of excrements

Supplementary Materials

Table S1. Selected literature on oxygen consumption in lakes and reservoirs, and proposed main drivers of the observed areal hyoplimnetic metabolism (AHM).

Article	Author	Source	Study site	Proposed AHM drivers
Development of oxygen deficits in 14 southern Ontario lakes	Lasenby, D.C.	Limnology and Oceanography 20 (6), 993-999 (1975)	14 Ontario lakes (Canada)	Secchi depth
Hypolimnion oxygen consumption in lakes: Discussion of productivity and morphometry effects	Charlton, M.N.	Canadian Journal of Fisheries and Aquatic Sciences 37 (10), 1531-1539 (1980)	Lake Erie (USA)	Chlorophyll, hypolimnion thickness, temperature
The areal hypolimnetic oxygen deficit: An empirical test of the model	Cornett, R.J.; Rigler, F.H.	Limnology and Oceanography 25 (4), 672-679 (1980)	Meta-analysis of 20-91 lakes (various locations)	Total phosphorus, primary production, Secchi depth
Hypolimnetic redox and phosphorus cycling in hypereutrophic Lake Sebasticook, Maine	Mayer, L.M.; Liotta, F.P.; Norton, S.A.	Water Research 16 (7), 1189-1196 (1982)	Lake Sebasticook (Maine, USA)	Reduced substrates from sediment
Hypolimnetic oxygen consumption in small lakes	Fulthorpe, R.R.; Paloheimo, J.E.	Canadian Journal of Fisheries and Aquatic Sciences 42 (9), 1493-1500 (1985)	28 Ontario lakes (Canada)	Hypolimnion thickness, organic carbon, iron
Hypolimnetic metabolism in Lake Washington: Relative effects of nutrient load and food web structure on lake productivity	Lehman, J.T.	Limnology and Oceanography 33 (6), 1334-1347 (1988)	Lake Washington (Washington, USA)	External nutrient input
Predicting changes in hypolimnetic oxygen concentrations with phosphorus retention, temperature, and morphometry	Cornett, R.J.	Limnology and Oceanography 34 (7), 1359-1366 (1989)	Meta-analysis of 41 temperate lakes (various locations)	Hypolimnion thickness, total phosphorus retention, substratum volume-to-sediment area ratio
Pelagic food web interactions and hypolimnetic oxygen depletion: Results from experimental enclosures and lakes	Mazumder, A.; McQueen, D.J.; Taylor, W.D.; Lean, D.R.S.	Aquatic Sciences 52 (2), 144-155 (1990)	Lake St. George, Haynes Lake (Canada)	Secchi depth, plankton size distribution

Table S1 (cont.)

Title	Authors	Reference	Study	Keywords
The prediction of hypolimnetic oxygen profiles: a plea for a deductive approach	Livingstone, D.M.; Imboden, D.M.	Canadian Journal of Fisheries and Aquatic Sciences 53 (4), 924-932 (1996)	Modelling study	Sediment oxygen demand, water column respiration
Hypolimnetic anoxia and sediment oxygen demand in California drinking water reservoirs	Beutel, M.W.	Lake and Reservoir Management 19 (3), 208-221 (2003)	9 reservoirs (California, USA)	Hypolimnion depth, chlorophyll, sediment oxygen demand
The dual influences of dissolved organic carbon on hypolimnetic metabolism: organic substrate and photosynthetic reduction	Houser, J.N.; Bade, D.L.; Cole, J.J.; Pace, M.L.	Biogeochemistry 64 (2), 247-269 (2003)	21 temperate lakes (North America)	External dissolved organic carbon input
Long-term changes in the areal hypolimnetic oxygen deficit (AHOD) of Onondaga Lake: Evidence of sediment feedback	Matthews, D.A.; Effler, S.W.	Limnology and Oceanography 51 (1), 702-714 (2006)	Onondaga Lake (New York, USA)	Particulate organic carbon, sediment oxygen demand
Evaluation of hypolimnetic oxygen demand in a large eutrophic raw water reservoir, San Vicente Reservoir, Calif.	Beutel, M.; Hannoun, I.; Pasek, J.; Kavanagh, K.B.	Journal of Environmental Engineering 133 (2), 130-138 (2007)	San Vicent Reservoir (California, USA)	Sediment oxygen demand
Hypolimnetic oxygen consumption by sediment-based reduced substances in former eutrophic lakes	Matzinger, A.; Müller, B.; Niederhauser, P.; Schmid, M.; Wüest, A.	Limnology and Oceanography 55 (5), 2073-2084 (2010)	Pfäffikersee and Türlersee (glacial lakes in Switzerland)	Reduced substrates from sediment
Hypolimnetic oxygen depletion in eutrophic lakes	Müller, B.; Bryant, L.D.; Matzinger, A.; Wüest, A.	Environmental Science and Technology 46 (18), 9964-9971 (2012)	Meta-analysis of 11 eutrophic lakes (Switzerland)	Sediment oxygen demand, reduced substrates from sediment
Potential impact of *Chironomus plumosus* larvae on hypolimnetic oxygen in the central basin of Lake Erie	Soster, F.M.; Matisoff, G.; Schloesser, D.W.; Edwards, W.J.	Journal of Great Lakes Research 41(2), 348-357 (2015)	Lake Erie (USA)	Oxygen uptake by chironomid burrows

Table S2. Respiration rates of *Chaoborus flavicans* larvae (instar 3–4) in terms of CO_2 production and O_2 consumption at different temperatures.

Trial	Number of *Chaoborus* larvae	Temperature (°C)		Respiration (μmol CO_2 ind^{-1} d^{-1})
1	35	22.5		1.87
2	17	23.1		1.85
3	70	23.1		1.78
4	35	23.1		1.96
			Mean	1.87
			s.d.	0.07
5	70	8.4		1.11
6	35	8.4		1.09
			Mean	1.10
			s.d.	0.01
Trial	Number of *Chaoborus* larvae	Temperature (°C)		Respiration (μmol O_2 ind^{-1} d^{-1})
7	99	20.7		2.21
8	100	8.4		1.12

Table S3. Estimated annual phosphorus flux into sediment due to excretion by burrowing *Chaoborus* as a function of depth and *Chaoborus* population density (instar 3-4). Highlighted numbers exceed the theoretical P loading needed to create mesotrophic (yellow), eutrophic (blue) or hypertrophic condition (red) (Shannon and Brezonik, 1972).

Mean hypolimnion depth (m)	*Chaoborus* population density (ind m^{-2})				
	2000	5000	10000	20000	50000
	P flux into sediment (g m^{-2} y^{-1})				
10	0.12	0.31	0.62	1.23	3.09
20	0.12	0.29	0.58	1.15	2.88
30	0.11	0.27	0.53	1.07	2.67
40	0.10	0.25	0.49	0.98	2.46
50	0.09	0.22	0.45	0.90	2.25
70	0.07	0.18	0.37	0.73	1.83