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1   Effects of water browning on freshwater biodiversity. The case of the predatory phantom midge

2   *Chaoborus nyblaei.*

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14   **Abstract**

15   Water browning, due to increased runoff of terrestrial dissolved organic carbon (DOC), has recently gained

16   considerable attention. While it is well settled how browning affects light regime and thereby aquatic primary

17   production, other impacts on the aquatic biota is less explored. Water browning shelters against UV radiation,

18   and may thus benefit range expansion of UV sensitive organisms, such as midges. We mapped occurrence of

19   Chaoborids in 148 subalpine and alpine ponds in Norway, and identified an apparent threshold for their presence

20   around 3 mg total organic carbon (TOC) l^{-1}. The field study was complemented with laboratory experiments on

21   *Chaoborus nyblaei* (Zetterstedt 1838), to test if this species is able to identify and select water colour

22   (concentrations of DOC) for oviposition. Number of egg rafts on brown water tanks was significantly higher

23   than in clear water tanks, indicating that *C. nyblaei* performs oviposition habitat selection. Chaoborids are

24   effective predators in planktonic habitats, and our findings support the hypothesis that climate change may

25   cascade through the ecosystem and promote range shifts of species due to alternated habitat frame conditions.

26   **Key words**

27   *Chaoborus nyblaei; oviposition choice; Dissolved Organic Carbon; climate change*

Introduction

Increased concentrations of dissolved organic carbon (DOC) and associated water browning is a growing concern in northern lakes and rivers (Kortelainen et al., 2006; Solomon et al., 2015). Reduced sulphate deposition (Monteith et al., 2007; Evans et al., 2012), increased temperatures and precipitation (Erlandsson et al., 2008; De Wit et al. 2016), longer growth seasons and higher terrestrial productivity (Larsen et al., 2011; Finstad et al., 2016) and elevated timberlines (Hofgaard et al., 2013) have all regionally been identified as contributors. Browning affects aquatic biota in multiple ways, in terms of productivity and interspecific competition (Williamson et al., 1999; Rautio & Tatarotti, 2010). It attenuates short-wave radiation both in the photosynthetic active region (PAR) and in the UV spectrum (Arts et al., 2000) and reduce area-specific primary production (Thrane et al., 2014), as well as secondary production (Karlsson et al., 2009; Finstad et al., 2013). However, browning also offers increased protection against harmful short-waved radiation, and could hence also facilitate for new predators (Wissel el al., 2003; Boeing et al., 2004). Possible candidates are phantom midges of the genus Chaoborus, as their transparent and predatory larvae are highly sensitive to UV-radiation and correspondingly responsive to increased shading (Persaud & Yan, 2003; Nagiller & Sommaruga, 2004). Phantom midges are planktonic top predators in the absence of fish (Neill, 1981; Yan et al., 1991) and may alter the planktonic community structure if introduced to new regions. *Chaoborus americanus* and *C. flavicans* were recently reported to extend their range across the cold Nearctic, directly or indirectly due to climate warming (Taylor et al., 2015), and Lindholm et al. (2016) found that *C. nyblaei* exerted strong effects on biodiversity in alpine ponds in association with recent browning. Range shifts in Chaoborids are hence possible examples for biotic cascading effects in the wake of global warming.

A behavioural prerequisite for successful range expansions is the ability to identify new suitable habitats, especially expressed as oviposition habitat choice. Such behaviour is widely recognized among insects, both in relation to offspring predator avoidance (Blaustein et al., 2004; Wiklund & Friberg, 2008; Resetarits & Silberbush, 2015; Segev et al., 2016), resource abundance (Fader & Juliano, 2014) and reduced intraguild competition (Allan & Kline, 1998; Zahiri & Rau, 1998). Among Chaoborids, habitat avoidance for oviposition is found to be associated with presence of fish or backswimmers (Petranka & Fakhoury, 1991; Berendonk, 1999; Berendonk & Bonshall, 2002). To what extent female Chaoborids are able to recognize other habitat features, for instance DOC, remains unknown, but their presence in shallow water bodies is mainly confined to coloured water, probably due to UV sensitivity of their transparent ("glassworms") larvae (Sommaruga, 2001; Boeing et

al., 2004; Nagiller & Sommaruga, 2009). The load of UV radiation (250-320 nm) increases with nearly 20 % per 1000 m elevation, making alpine ponds particularly prone to such stress (Blumentaler et al., 1992). These waterbodies are typically lower in DOC owing to sparsely developed catchment vegetation. Low temperatures will further slow down cellular repair mechanisms that are coping with UV-induced damage, and typically alpine invertebrates have high levels of photoprotective pigments like melanin, carotenoids or mycosporine-like amino acids (MAAS) (Hessen and Sørensen, 1990; Sommaruga et al., 1999). While the conspicuous lack of visible pigments is evident in the transparent larvae of Chaoborus (likely an antipredator strategy to reduce visibility), the presence of MAAS of efficient anti-oxidants (Lopez-Martinez et al., 2008) remains unsettled. Previous tests do however confirm a strong UV-susceptibility assessed as DNA-damage by Comet assay (Lindholm et al. 2016).

The large (23 mm long larvae) *Chaoborus nyblaei* (Zetterstedt 1838) inhabits European small ponds and puddles (Hirvenoja, 1961; Nilssen, 1974; Borkent, 1979; 1981) and could clearly benefit from water browning and extend its range into former clear water systems, especially above the timberline. *C. nyblaei* was recently found in Norwegian alpine ponds close to 1200 masl (Lindholm et al., 2016). These populations suffered from severe DNA damage, however, indicating that they persist close to their tolerance threshold. Using a 30 year time series for increased in Normalized Difference Vegetation Index (NDVI) as proxy for increased vegetation cover and according increased water browning (Finstad et al., 2016), this study claimed that browning possibly explained a recent introduction of *C. nyblaei* in these alpine environments.

This study quantifies the increase of water browning and explores shading effects in boreal and alpine shallow ponds, focussing on occurrence and possible range extension of Chaoborids. Field data were substantiated by lab experiments, where we tested if oviposition habitat choice of female *C. nyblaei* was affected by increased DOC concentration. Our study has some relevance for the potential for predacious Chaoborids to extend their range of distribution in the shades of increased water browning, and thereby alter local biodiversity.

Methods

The field study was conducted in ponds located in two montane and alpine regions of southern Norway, at Dovre (74 ponds) and Vassfaret (74 ponds) during June and July 2016, covering an elevational span from 750 to 1400 meters above sea level, with the timberline at approximately 1000 masl. All ponds were small (10 m^2 - 5 ha), shallow (0,1 - 2 m) and devoid of fish. Samples for total organic carbon were taken well off the shoreline,

88   possibly at 0,5 m depth, kept dark on 100 ml brown glass bottles and stored cold, brought to the lab and analysed

89   for TOC by a Shimadzu 5050 analyser. The dissolved fractions of carbon in general comprise some 95% of TOC

90   in Norwegian lakes (Larsen et al., 2011) and TOC and DOC are thus in practice interchangeable. In order to test

91   if DOC is a reliable parameter for water browning and shading were the Vassfaret ponds in addition analysed for

92   UV absorbance at $\lambda 254$, by use of standard spectrophotometric method and a quartz cuvette (as a measure of

93   water transparency to UV-radiation; Brandstetter et al. 1996). The transparency of the Vassfaret ponds was also

94   assessed by means of a relative scale of color (mg Pt/L) for comparison with data from the same localities

95   analysed during June and July 1968 (Eie 1974) by this method, hence allowing us to calculate the increase of

96   browning for the last 48 years. The same localities were also analysed for DOC to verify the validity of the Pt-

97   standard as a proxy of organic C. Yearly data on TOC collected from six lakes in the vicinity of Vassfaret for the

98   period from 1983 to 2013 (published in Finstad et al. 2016) was applied to substantiate possible long term trends

99   in TOC concentration (data shown in Appendix).

100   Presence of Chaoborus sp. was examined by towing a standard plankton net (Ø40 cm, 100 cm long) three times

101   across each pond, in order to identify their clear water tolerance threshold in terms of DOC (see Table 1 for basic

102   physico-chemical properties of the ponds). As certain species may dwell in the sediments during daytime

103   (Davidovicz et al., 1990), especially in clear water systems where UV radiation act as a potent stressor, bottom

104   sediments were stirred by wading while sampling. Night sampling was conducted for a subset of ponds for the

105   same reason, but did not provide additional records of Chaoborids. Observations on other predacious

106   invertebrates were limited to single records of Dytiscid larvae, leaving Chaoborids as the dominant pelagic top

107   predator of these otherwise species poor systems.

108   The selection of sites for oviposition in *C. nyblaei* related to water colour was tested in an 18 m² climate

109   chamber at +17 °C, illuminated with 6 standard white 13 W fluorescence ceiling lights. The chosen temperature

110   was within the range (14 – 21 °C) measured at the actual pond from where pupas for the experiment were

111   collected. Pupas were obtained by use of a dip net and kept in a white plastic tray at the shore. 1000 pupas were

112   carefully transferred to 5 L vials by use of a large pipet, kept cold and dark and transported to the climate

113   chamber for hatching. The 5 L vials were kept in a 60 x 40 x 60 large cage sealed with mosquito net for

114   hatching. Newly hatched imagoes were released from the cage into the climate chamber every second day, to

115   prevent them to oviposit in the hatching trays. Walls were carefully sprayed every third day with water to

116   maintain humidity, but otherwise no food (i.e. sugar) were added. Nine water tanks, each 60 x 35 x 25 cm and

117   containing 10 L water were offered as oviposition sites: Three tanks were filled with clear water (DOC

118 concentration < 0.1 mg/L), another three with the same water, but enriched with natural, organic matter from a

119 humic lake, isolated by reverse osmosis and subsequently freeze-dried to a "humus powder" (details in Hessen &

120 Færøvig 2001) to a final concentrations of 30 mg DOC l^{-1}, and three tanks with natural water (18.2 mg DOC l^{-1})

121 from a forest pond. DOC concentrations were analysed at onset of the experiment. The position of the tanks in

122 the climate chamber was randomized, and minimum distance between tanks were 30 cm. The experiment was

123 run for three weeks, before floating egg rafts in each tank were counted. To test whether egg-laying differed

124 between the three treatments, we modelled the number of eggs as a function of DOC treatment using a

125 generalized linear model with a Poisson distribution and a log-link. We used a Poisson distribution because the

126 response variable contains count data. DOC concentration was treated as a factor variable with three levels.

127 **Results**

128 Comparing water color (mg Pt/L) in 1968 with 2016 revealed a significant increase (p<<0.01, Wilcoxon signed

129 rank; fig. 1, upper panel). The average increase below the timberline was 20 mg Pt/L, while the alpine region

130 showed a more modest increase (6 mg Pt/L). Time series on TOC from six lakes in the vicinity of Vassfaret

131 sampled yearly from 1983 to 2013 revealed a corresponding pattern (Table 1, Appendix). Measurements of UV

132 absorbance at λ254, moreover, clearly showed that TOC was a accurate proxy for UV attenuation in this systems

133 (r^2=0.987; Fig 1, middle). Data on TOC from all 148 ponds spanned from 0.4 to 19.2 mg DOC/L (Fig 1, lower),

134 hence including both typical clear ponds and strongly coloured water bodies. Concentrations were weakly

135 correlated with elevation, but were generally highest below the timberline, reflecting the higher terrestrial

136 productivity and thus higher export of TOC. Chaoborids (i.e., *C. flavicans, C. crystallinus, C. obscuripes, C.*

137 *nyblaei*) occurred in 28 of the 148 ponds. TOC was a significant explanatory variable for their presence, as

138 chaborids never were recorded at concentrations < 3.5 mg DOC l^{-1} (logistic regression, *p*-value 4.763 1.91e-06

139 ***). Only *C. nyblaei* was found above the timberline (at approximately 1000 masl). Three of these ponds were

140 quite shallow (< 0.3 m max depth), and larvae were found only after stirring the bottom sediments.

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142 Figure 1. Upper left: Water colour (mg Pt/L) for 74 ponds from Vassfaret increased significantly from 1968 to

143 2016 (p<<0.01, Wilcoxon signed rank). Upper right: Correlation of TOC to UV absorbance at λ254 (r^2=0.987).

144 Below: 148 ponds of various altitudes (masl) and TOC concentration (mg/L) explored for presence (black dots)

145 and absence (open dots) of Chaoborus sp. All ponds with Chaoborus sp. had DOC concentrations > 3,5 mg/L

146 (marked with vertical dotted line; logistic regression, *p*-value < 0,001).

147   To clarify whether Chaoborus actively select high-DOC localities for oviposition, we conducted a laboratory

148   experiment to test for oviposition habitat preferences in accordance to water colour, by offering ovipositioning

149   female *C. nyblaei* both clear and coloured water for reproduction. As judged from a Poisson distribution model,

150   there was a significant difference in preference for oviposition in brown water over clear water (Fig 2, Table 2).

151   The average number of egg rafts in clear water was 4 (median: 3), compared to 8 (median: 7) in the artificial

152   DOC water and 8 (median: 8) in the natural DOC water. There were no differences between water artificially

153   brownified with freeze dried DOC powder and natural DOC rich water, although many volatile carbon

154   substances and organic oil fraction could have been altered during dry freezing.

155

156   Figure 2. Results of experimental oviposition choice of *Chaoborus nyblaei* from the climate chamber. Number of

157   egg rafts laid on clear water (< 0.1 mg DOC/L, n=3; left), on natural TOC rich forest pond water (18.2 mg

158   DOC/L, n=3; middle), and on brownified clear water (added 30 mg DOC/L, n=3; right). Horizontal lines mark

159   average values.

160

161   Table 2: Estimates, confidence intervals, and *p*-values from the generalized linear model (glm) of the number of

162   eggs as function of TOC treatment. Since the response variable is log-transformed, we present the back-

163   transformed estimates (i.e., the exponentials of the estimates). The estimate for the intercept thus represents the

164   predicted number of eggs in the clear water treatment. Upper and lower confidence limits are also presented. The

165   corresponding values for the two TOC-treatments represents the estimated relative difference between the given

166   treatment and the clear water treatment. The model residual deviance was 7.8884 on 6 df; n = 9.

167   **Discussion**

168   This study is consistent with trends of browning that has been seen over many northern areas (Monteith et al.

169   2007; de Wit et al. 2017; Meyer-Jacob et al. 2017), and that in northern boreal areas also is associated with

170   increased terrestrial vegetation (Larsen et al. 2011; Finstad et al. 2016). TOC data from six lakes in the vicinity

171   of Vassfaret in the last mentioned study reflect a rather monotonous increase for the actual period (Table 1;

172   Appendix). Using sediment cores, Meyer-Jacob et al. (2017) found a corresponding gradual increase in TOC in

173   lakes across Canada, Greenland and northern Europe. While this has been linked to decreased ecosystem

174   productivity owing to increased light attenuation (Karlsson et al. 2009; Thrane et al. 2014), we here also provide

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175   evidence for a subtler biotic impact promoted by increased attenuation of harmful short-wave radiation. The

176   survey over a wide range of fish-free high latitude sites suggest 3.5 mg DOC/L as an approximately threshold for

177   the presence of Chaoborids. It should be noted that this level does not strictly correlate with altitude, e.g. it is

178   unlikely to be an altitude (or rather temperature) effect in disguise. The level, however, corresponds closely to

179   previous analysis of extensive DNA damage in *C. nyblaei* in alpine ponds at TOC concentrations of 3.9 mg/L

180   (Lindholm et al., 2016).

181   The attenuation of short-wave radiation, and notably UV-B, decreases exponentially when DOC concentrations

182   drop below 3 mg/L (Scully & Lean, 1994; Laurion et al., 1997; Thrane et al., 2014), leading to a corresponding

183   accelerating increase in DNA damage (Wolf et al., 2017). The effect is enhanced in alpine shallow ponds both

184   due to intensified UV-B load (Blumentaler et al., 1992) and the lack of deeper sheltering refugia. Low

185   temperatures are likely to slow down photorepair capacity, too. It thus seems probable that water transparency

186   (and depth) are main factor constraining the range of phantom midges in alpine clear water bodies (Boeing et al.,

187   2004; Nagiller & Sommaruga, 2009), and the further browning of boreal and arctic regions will probably

188   facilitate for range extensions of such UV sensitive predators, with subsequent effects on planktonic biodiversity

189   (Lindholm et al., 2016). Our findings are in line with Taylor et al. (2015) who found that Nearctic Chaoborids

190   recently have extended their range northwards with 500 km, due to tundra snow-melt dams.

191   A considerable body of literature reports on oviposition choice and habitat preferences on aquatic insects

192   (Resetarits, 1996; Reiskind & Wilson, 2004; Fader & Juliano, 2014), and both visual, olfactory and tactile

193   responses are known. Species which deposit their egg rafts on the water surface are shown to use tactile stimuli

194   in order to evaluate water properties prior to oviposition (Bentley & Day, 1989). Asmare et al. (2017) found that

195   *Anopheles arabiensis* preferred volatiles from water submerged Poaceae grasses over *Thypha latifolia*, pointing

196   to subtle sensory abilities to recognize organic substances. Our laboratory experiment clearly supports the

197   hypothesis that *C. nyblaei* is able to identify differences in local TOC concentration, and to choose oviposition

198   site accordingly. Such oviposition preference is clearly an evolutionary more rewarding strategy than random

199   oviposition with major losses of eggs and larvae due to predation of UV-exposure. These findings are also in line

200   with previous studies, demonstrating that Chaoborids avoid ponds of fish or backswimmers (Petranka &

201   Fakhoury, 1991; Berendonk, 1999; Berendonk & Bonshall, 2002).

202   Oviposition habitat choice is surely only one factor which affect the success rate of range extensions. Chaoborids

203   are susceptible to fish predation, and generally depend on hypolimnetic refugia to avoid visual fish predation

204 (Davidowicz 1990). *C. nyblaei* is considered as a pond dweller, with assumed dry resistant eggs adapted to

205 desiccation and temporal ponds (Borkent 1979), typically devoid by fish. This could explain the considerable

206 size of the larvae, as well, which are the largest of the genus (Saether 1972). Fish were absent in all ponds

207 included in this study. There is a general agreement that Chaoborids under such conditions constitute the top

208 predators in pelagic food webs, both due to high densities and because other invertebrate predators (water beetles

209 of the genus Dytiscus, Odonathe nymphs) mainly feed on benthic prey and hardly affect pelagic food chains

210 (Pritchard, 1965; Van Buskirk, 1988; Cobbaert et al., 2010).

211 Our findings demonstrate a subtle and indirect impact of browning, which again at least partly is a consequence

212 of climate change and ecosystem responses in alpine areas. We provide support for the assumption that

213 Chaoborids may take advantage of the ongoing water browning processes observed in northern watersheds and

214 extend their range accordingly. Chaoborid larvae are effective predators with substantial effects on local

215 biodiversity (Lynch, 1979), sometimes able to drive prey communities to extinction (Lindholm et al., 2016). Our

216 data hence points to possible intriguing cascading effects of global warming on aquatic biodiversity in shallow

217 montane and alpine ponds, where increased browning may facilitate for range extension of new, otherwise UV

218 sensitive species, with substantial consequences on local biodiversity.

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