Possible range extension of the predatory phantom midge *Chaoborus nyblaei* mediated by water browning

Markus Lindholm1,2,\*, Martin Eie3, Dag Olav Hessen3, Joachim Tørum Johansen1, Kristoffer Weiby4 and Jens Thaulow1

1Norwegian Institute for Water Research (NIVA), Gaustadalléen 21, 0349 Oslo, Norway

2Rudolf Steiner University College, Prof. Dahls gate 30, N-0260 Oslo, Norway

3University of Oslo, P.O. Box 1066 Blindern, N-0316 Oslo, Norway

4Norwegian University for Life Sciences/NMBU, N-1432 Ås, Norway

\*Corresponding author: Markus Lindholm, Markus.Lindholm@niva.no

**Abstract**

Water browning, due to increased runoff of terrestrial dissolved organic carbon (DOC), has recently gained considerable attention. While it is well settled how browning affects light regime and thereby aquatic primary production, other impacts on the aquatic biota is less explored. Water browning shelter against UV radiation, and may thus benefit range expansion of UV sensitive organisms, such as midges. We mapped occurrence of Chaoborids in 148 subalpine and alpine ponds in Norway, and identified an apparent threshold for their presence around 3 mg total organic carbon (TOC) l-1. The field study was complemented with laboratory experiments on *Chaoborus nyblaei* (Zetterstedt 1838), to test if this species is able to identify and select water colour (concentrations of DOC) for oviposition. Number of egg rafts on brown water tanks was significantly higher than in clear water tanks, indicating that *C. nyblaei* performs oviposition habitat selection. Chaoborids are effective predators in planktonic habitats, and our findings support the hypothesis that climate change may cascade through the ecosystem and promote range shifts of species due to alternated habitat frame conditions.

**Key words**

*Water browning; 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). DOC attenuates short-wave radiation both in the photosynthetic active region (PAR) and in the UV spectre (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). DOC efficiently attenuates UV and may induce formation of free radicals in the very surface (Wolf et al. 2017). However, it offers increased protection against harmful short-waved radiation, too, 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 anyway 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 *Chaoborus 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 *Chaoborus 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 m2 - 5 ha), shallow (0,1 - 2 m) and devoid by fish. Ponds were analysed for total organic carbon (TOC) by a TOC Shimadzu 5050 analyser. The dissolved fractions of carbon in general comprise some 95% of TOC in Norwegian lakes (Larsen et al., 2011) and TOC and DOC are thus in practice interchangeable. In order to test if DOC is a reliable parameter for water browning and shading were the Vassfaret ponds in addition analysed for UV absorbance at λ254 (as a measure of water transparency to UV-radiation; Brandstetter et al., 1996). The transparency of the Vassfaret ponds was also assessed my means of a relative scale of color (mg Pt/L) for comparison with data from the same localities analyzed during June and July 1968 (Eie 1974) by this method, hence allowing us to calculate the increase of browning for the last 48 years. The same localities were also analysed for DOC to verify the validity of the Pt-standard as a proxy of organic C.

Presence of Chaoborus sp. was examined by towing a plankton net three times across each pond, in order to identify their clear water tolerance threshold in terms of DOC. As certain species may dwell in the sediments during daytime (Davidovicz et al., 1990), especially in clear water systems where UV radiation performs a potent stressor, bottom sediments were stirred by wading while sampling. Night sampling was conducted for a subset of ponds, but did not provide additional records. Observations on other predacious invertebrates were limited to single records of Dytiscid larvae, leaving Chaoborids as the dominant pelagic top predator of these otherwise species poor systems.

The selection of sites for oviposition in *Chaoborus nyblaei* related to water colour was tested in an 18 m2 climate chamber at +17 °C. The chosen temperature was within the range (14 – 21 °C) measured at the actual pond from where pupas for the experiment were collected. Pupas were gained by use of a dip net and kept in a white plastic tray at the shore. 1000 pupas were carefully transferred to 5 L vials by use of a large pipet, kept cold and dark and transported to the climate chamber for hatching. The 5 L vials were kept in a 60 x 40 x 60 large cage sealed with mosquito net for hatching. Newly hatched imagoes were released from the cage into the climate chamber every second day, to prevent imagoes to lay eggs in the hatching trays. Nine water tanks, each 60 x 35 x 25 cm and containing 10 L water were offered as oviposition sites: Three tanks were filled with clear water (DOC concentration < 0.1 mg/L), another three with the same water, but enriched with natural, organic matter from a humic lake, isolated by reverse osmosis and subsequently freeze-dried to a “humus powder” (details in Hessen & Færøvig 2001) to a final concentrations of 30 mg DOC l-1, and three tanks with natural water (18.2 mg DOC l-1) from a forest pond. The position of the tanks in the climate chamber was randomized, and minimum distance between tanks were 30 cm. The experiment was run for three weeks, before floating egg rafts in each tank were counted. To test whether egg-laying differed between the three treatments, we modelled the number of eggs as a function of DOC treatment using a generalized linear model with a Poisson distribution and a log-link. We used a Poisson distribution because the response variable contains count data. DOC concentration was treated as a factor variable with three levels.

**Results**

Comparing water color (mg Pt/L) in 1968 with 2016 revealed a significant increase (p<<0.01, Wilcoxon signed rank; fig. 1, upper panel). The average increase below the timberline was 20 mg Pt/L, while the alpine region showed a more modest increase (6 mg Pt/L). Measurements of UV absorbance at λ254, moreover, clearly showed that TOC was a accurate proxy for UV attenuation in this systems (r2=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), hence including both typical clear ponds and strongly coloured water bodies. Concentrations were weakly correlated with elevation, but were generally highest below the timberline, reflecting the higher terretsrial productivity and thus higher export of TOC. Various species of *Chaoborus* sp. (i.e., *C. flavicans, C. crystallinus, C. obscuripes, C. nyblaei*) were found in 28 ponds, from boreal forest ponds to high alpine habitats close to 1200 m. TOC was a significant explanatory variable for their presence, as chaborids never were recorded at concentrations < 3.5 mg DOC l-1 (logistic regression, *p-*value 4.763 1.91e-06 \*\*\*). Only *C. nyblaei* was found above the timberline (at approximately 1000 masl). Three of these ponds were quite shallow (< 0.3 m max depth), and larvae were found only after stirring the bottom sediments.

Figure 1. Upper left: Water colour (mg Pt/L) for 74 ponds from Vassfaret increased significantly from 1968 to 2016 (p<<0.01, Wilcoxon signed rank). Upper right: Correlation of TOC to UV absorbance at λ254 (r2=0.987). Below: 148 ponds of various altitudes (masl) and TOC concentration (mg/L) explored for presence (black dots) and absence (open dots) of Chaoborus sp. All ponds with Chaoborus sp. had DOC concentrations > 3,5 mg/L (marked with vertical dotted line; logistic regression, *p-*value < 0,001.

To clarify whether Chaoborus actively select high-DOC localities for oviposition, we conducted a laboratory experiment to test for oviposition habitat preferences in accordance to water colour, by offering ovipositioning female *C. nyblaei* both clear and coloured water for reproduction. As judged from a Poisson distribution model, there was a significant difference in preference for oviposition in brown water over clear water (Fig 2, Table 1). The average number of egg rafts in clear water was 4 (median: 3), compared to 8 (median: 7) in the artificial DOC water and 8 (median: 8) in the natural DOC water. There were no differences between water artificially brownified with freeze dried DOC powder and natural DOC rich water, although many volatile carbon substances and organic oil fraction could have been altered during dry freezing.

Figure 2. Results of experimental oviposition choice of *Chaoborus nyblaei* from the climate chamber. Number of egg rafts laid on clear water (< 0.1 mg DOC/L, n=3; left), on natural TOC rich forest pond water (18.2 mg DOC/L, n=3; middle), and on brownified clear water (added 30 mg DOC/L, n=3; right). Horizontal lines mark average values.

Table 1: Estimates, confidence intervals, and *p*-values from the generalized linear model (glm) of the number of eggs as function of TOC treatment. Since the response variable is log-transformed, we present the back-transformed estimates (i.e., the exponentials of the estimates). The estimate for the intercept thus represents the predicted number of eggs in the clear water treatment. Upper and lower confidence limits are also presented. The corresponding values for the two TOC-treatments represents the estimated relative difference between the given treatment and the clear water treatment. The model residual deviance was 7.8884 on 6 df; n = 9.

**Discussion**

This study confirms the trend of browning that has been seen over many northern areas (Monteith et al. 2007; de Wit et al. 2017), and that in northern boreal areas also is associated with increased terrestrial vegetation (Larsen et al. 2011; Finstad et al. 2016). While this has been linked to decreased ecosystem productivity owing to increased light attenuation (Karlsson et al. 2009; Thrane et al. 2014), we here also provide evidence for a subtler biotic impact promoted by increased attenuation of harmful short-wave radiation. The survey over a wide range of fish-free high latitude sites clearly suggest 3.5 mg DOC/L as an approximately threshold for the presence Chaoborus. It should be noted that this level does not strictly correlate with altitude, e.g. it is unlikely to be an altitude (or rather temperature) effect in disguise. The level corresponds to previous analysis of extensive DNA damage in *C. nyblaei* in alpine ponds at TOC concentrations of 3.9 mg/L (Lindholm et al., 2016).

The attenuation of short-wave radiation, and notably UV-B, decreases exponentially when DOC concentrations drop below 3 mg/L (Scully & Lean, 1994; Laurion et al., 1997; Thrane et al., 2014), leading to a corresponding accelerating increase in DNA damage (Wolf et al., 2017). The effect is enhanced in alpine shallow ponds both due to intensified UV-B load (Blumentaler et al., 1992) and the lack of deeper sheltering refugia. Low temperatures are likely to slow down photorepair capacity, too. It thus seems probable that water transparency (and depth) are main factor constraining the range of phantom midges in alpine clear water bodies (Boeing et al., 2004; Nagiller & Sommaruga, 2009), and the further browning of boreal and arctic regions will promote range extensions of such UV sensitive predators with subsequent effects on planktonic biodiversity (Lindholm et al., 2016). Our findings are in line with Taylor et al. (2015) who found that Nearctic Chaoborids recently have extended their range northwards with 500 km, due to tundra melt and tow dams.

A considerable body of literature reports on oviposition choice and habitat preferences on aquatic insects (Resetarits, 1996; Reiskind & Wilson, 2004; Fader & Juliano, 2014), and both visual, olfactory and tactile responses are known. Species which deposit their egg rafts on the water surface are shown to use tactile stimuli in order to evaluate water properties prior to oviposition (Bentley & Day, 1989). Asmare et al. (2017) found that *Anopheles arabiensis* preferred volatiles from water submerging Poaceae grasses over *Thypha latifolia*, pointing to subtle sensory abilities to recognize organic substances. Our laboratory experiment clearly supports the hypothesis that *Chaoborus nyblaei* is able to identify differences in local TOC concentration, and to choose oviposition site accordingly. These findings are also in support of with previous studies, demonstrating that Chaoborids avoid ponds of fish or backswimmers (Petranka & Fakhoury, 1991; Berendonk, 1999; Berendonk & Bonshall, 2002). Such oviposition preference is clearly an evolutionary more rewarding strategy than random oviposition with major losses of eggs and larvae due to predation of UV-exposure.

Oviposition habitat choice is surely only one factor which affect the success rate of range extensions. Chaoborids are susceptible to fish predation, and generally depend on hypolimnetic refugia to avoid visual fish predation (Davidowicz 1990). *C. nyblaei* is considered as a pond dweller, with assumed dry resistant eggs adapted to desiccation and temporal ponds (Borkent 1979), typically devoid by fish. This could explain the considerable size of the larvae, as well, which are the largest of the genus (Saether 1972). Fish was absent in all ponds included in this study. There is a general agreement that Chaoborids under such conditions constitute the top predators in pelagic food webs, both due to high densities and because other invertebrate predators (water beetles of the genus Dytiscus, Odonathe nymphs) mainly feed on benthic prey and hardly affect pelagic food chains (Pritchard, 1965; Van Buskirk, 1988; Cobbaert et al., 2010).

Our findings demonstrate a subtle and indirect impact of browning, which again at least partly is a consequence of climate change and ecosystem responses in alpine areas. We provide support for the assumption that Chaoborids may take advantage of the ongoing water browning processes observed in northern watersheds and extend their range accordingly. Chaoborid larvae are effective predators with substantial effects on local biodiversity (Lynch, 1979), sometimes able to drive prey communities to extinction (Lindholm et al., 2016), and our data hence points to a intriguing cascading effect of global warming on aquatic biodiversity in shallow montane and alpine ponds.

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Michael H. Reiskind

Department of Ecology and Evolutionary Biology, The University of Michigan, Ann Arbor, MI 48109

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