Water Browning Influences the Behavioral Effects of Ultraviolet Radiation on Zooplankton

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In the last decades, limnic water bodies in the Northern hemisphere have experienced a noticeable browning, i.e., increasing levels of dissolved organic matter (DOM). While the effects on primary producers is usually considered negative (light attenuation), zooplankton is thought to benefit from increased DOM, which absorbs harmful ultraviolet radiation (UVR). However, behavioral alterations due to browning in zooplankton have not yet been studied. We investigated the effects of a DOM gradient, alone and in combination with UVR, on the swimming behavior of *Daphnia magna*. Making use of a computer-controlled imaging system, we repeatedly filmed individuals over 6 h and analyzed the video material to unravel effects on exploration behavior and other motility patterns. The results show that increasing DOM buffers the detrimental effects of UVR on swimming behavior. This is likely due to attenuation of UVR by DOM. Interestingly, DOM also raised the overall swimming activity independent of UVR exposure. Our findings highlight the importance of DOM in freshwater systems, not only because of its physico-chemical properties, but also due to its higher-level effects on zooplankton communities.

Keywords: behavioral traits, *Daphnia magna*, dissolved organic matter, ultraviolet radiation, video imaging

INTRODUCTION

In the Anthropocene's world of a changing climate (IPCC, 2014), wildlife throughout ecosystems has to cope with an increasing dissonance of altered bio-, geo-, and photo-chemical realities. In limnic systems of the Northern hemisphere, climate change manifestations are manifold (Adrian et al., 2009; Williamson et al., 2009). Amongst other observable changes, increases of dissolved organic matter (DOM) have led to an increased "browning" of waters in the recent past (Erlandsson et al., 2008; Solomon et al., 2015; Rantala et al., 2016). Reasons for this include climate change (Larsen et al., 2011; de Wit et al., 2016), increased land use (Evans et al., 2012; Arvola et al., 2017), and decreased sulfur deposition (Finstad et al., 2016; Monteith et al., 2017; Strock et al., 2017).

One of the main consequences of rising DOM is the increased attenuation of light. This can have direct negative results for primary producers, which rely on photosynthetically active radiation (Thrane et al., 2014). However, DOM also absorbs harmful ultraviolet radiation (UVR; Williamson et al., 2015). Especially for zooplankton residing in browning waters, the net result of increased DOM levels is thus seen as primarily positive. This is largely due to photoprotection from UVR, which is known to be harmful *via* a range of mechanisms, including direct DNA damage, protein denaturation and lipid peroxidation (Pellegri et al., 2014; Tartarotti et al., 2014). Interactions between DOM and UVR have been shown to affect growth and survival of zooplankton, as well as inducing DNA damages (Rautio and Korhola, 2002; Geddes, 2009; Wolf et al., 2017).

Zooplankton species are known to rapidly adapt their behavior to changes in the environment. Behavior is one of the first reactions to changes in the environment, having both effects on species interactions as well as individual fitness, and hence influencing the entire ecosystem's ecology (Sih et al., 2010). The behavioral responses of zooplankton to UVR are diverse and have been studied extensively (Rose et al., 2012; Hylander and Hansson, 2013). Exemplary adaptations in zooplankton behavior include predator avoidance (Lampert, 1989), grazing migration (Lampert and Taylor, 1985; Reichwaldt et al., 2004), and flight from UVR (Rhode et al., 2001; Williamson et al., 2001; Hylander and Hansson, 2010). However, behavioral effects of DOM—alone and in combination with UVR—have not been subject to investigation.

In this study, we seek to unravel the behavioral effects of DOM and its interaction with UVR on zooplankton. *Daphnia* species have a central role in the limnic food web, linking primary production with higher trophic levels, and can be found across all climates ranges. They are directly affected by changes in their environment, e.g., increased DOM and UVR. In natural systems, changes in swimming behavior affect several fitness-related traits, e.g., filter feeding, energy demand, and predator avoidance. We used a battery of endpoints as proxies for swimming activity. In particular, we measured the explored area, average swimming speed, median swimming depth, gross traveled distance, and swimming time. We used a customizable automated imaging solution to record and analyse movies, in order to dissect the effects of DOM, and its interaction with UVR, on zooplankton behavior.

MATERIALS AND METHODS

Animal Husbandry

For husbandry, *Daphnia magna* were reared in aerated full silicate glass aquaria with densities not exceeding 20 animals per liter. They were kept in filtered tap water (0.22 μm polyether sulfone filter; Corning, Corning, NY, USA), enriched to 4 mM $CaCl_2$, 4 mM $NaHCO_3$, 12 nM H_2SeO_3, and supplemented with vitamins B_{12}, D-biotin, and thiamine hydrochloride (4, 2, and 300 nM, respectively). Animals were cultured in a 16:8 h light:dark cycle at a light intensity of 1,500 lux (L 18 W/950 fluorescent lamps; OSRAM, Munich, Germany) and fed *Chlamydomonas reinhardtii* at an *ad libitum* diet.

The *D. magna* clone (DHI strain) of this study was originally obtained from the Norwegian Institute for Water Research (NIVA; Oslo, Norway) and has been cultured in our facilities without observable signs of stress over the last 4 years.

Experimental Setup

Gradients of DOM (2, 2.5, 5, 10, and 20 mg C L^{-1}) were prepared by dissolving freeze-dried Nordic Aquatic Humic Acid Reference (isolated from lake water using reverse osmosis; Gjessing et al., 1999) in *D. magna* culture medium; 2 mg C L^{-1} were the background concentration the *D. magna* culture medium. The concentrations were confirmed using a TOC-V$_{CPH}$ Total Organic Carbon Analyzer (Shimadzu, Kyoto, Japan).

The day before the experiment, adult daphnids carrying their third brood were isolated and left spawning overnight. Shortly before the start of the experiment the next day, individual neonates (not older than 24 h) were placed in 40 ml of the respective DOM-enriched *D. magna* culture medium in non-coated cell culture flasks (TC Flask T25, Suspension; Sarstedt, Nümbrecht, Germany). The water depth in these flasks was 4 cm. Duplicates of DOM treatments (ten flasks in total) were randomly placed in a row into the filming setup.
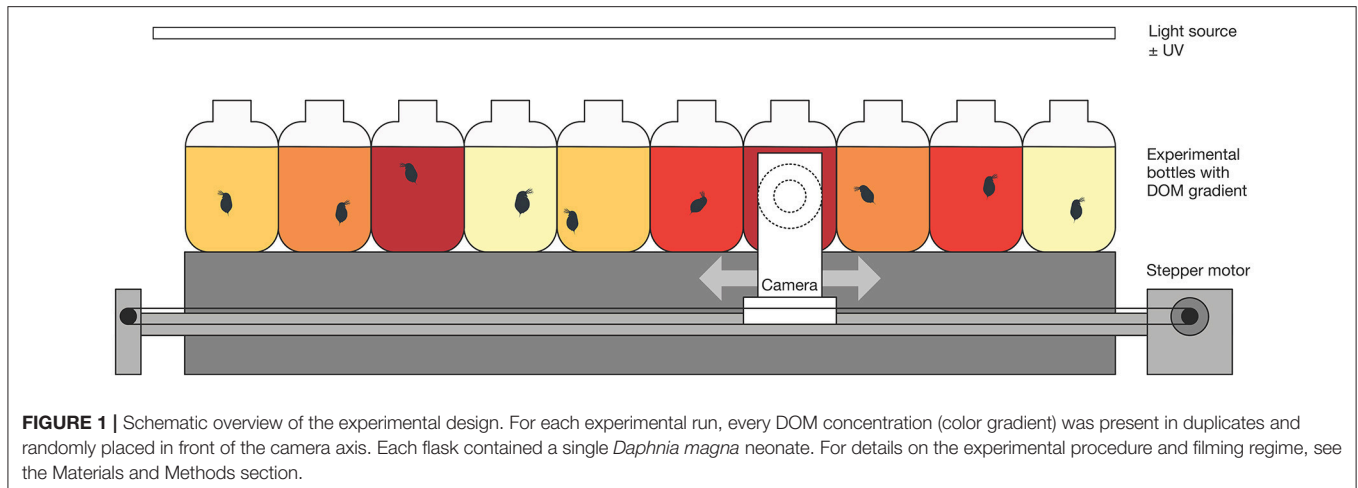
Flasks were illuminated from above either using the same *D. magna* light source as used for husbandry, or in combination with ultraviolet radiation (UVA-340 Lamp; Q-Lab, Westlake, OH, USA). The light source was chosen because it allowed easy manipulation of the photon flux spectrum, and because its waveband peak at 340 nm is sufficiently close to the environmentally relevant UVB waveband (Häder et al., 2011). During the non-UV treatments ("–UV"), daphnids received an intensity of 1,500 lux of regular light (OECD, 2012). The UV treatment ("+UV") was provided by substituting 60 μmol m^{-2} s^{-1} of the total light intensity of 1,500 lux with UVA$_{340}$ radiation ($\lambda = 340$ nm). Light intensities were calibrated with a SpectraPen LM 500-UVIS spectroradiometer (Photon Systems Instruments, Drásov, Czech Republic). The photon flux profiles are given in Supplementary Figure 1.

Each of the 10 bottles was filmed one at a time, using a moveable camera (Raspberry Pi NoIR Camera; Raspberry Pi Foundation, Cambridge, United Kingdom) mounted on a computer-controlled platform (Raspberry Pi; Raspberry Pi Foundation). Each experiment lasted 6 h, with each flask being filmed for 1 min at 26 frames per second every 19 min, resulting in 19 videos per flask. Each experiment was replicated three times with and without UV, resulting in six replicates per treatment combination. A custom Python script (version 2.7.13; available online at: https://www.python.org/; Supplementary Data 1) controlled the connected stepper motor (PhidgetStepper Bipolar HC; Phidgets, Calgary, Canada) and camera. A schematic overview of the experimental design is given in **Figure 1**.

Immediately following the experiments, all animals were post-fixed in 1% (v/v) Lugol's iodine and their size measured as core body length (Ranta et al., 1993) using digital image analysis tool Fiji (version 2.0.0-rc-43/1.51p; Schindelin et al., 2012).

Movie and Tracking Evaluation

The recorded video sequences were analyzed for movement behavior using a custom python script using the Open Source Computer Vision Library (OpenCV; version 3.3.0; available online at: http://opencv.org) to track individual animals. The script identifies the position of the individual *Daphnia* in the bottle and extracts its position (XY coordinates) for each frame. The annotated script is available in the online version of the article (Supplementary Data 2). The field of view of the camera included the whole waterbody. Due to the use of a rolling average for background subtraction during the feature extraction, individuals were not traced while they remained stationary for a prolonged time (>10 s). Missing positions were thus classified as resting. Position data were then imported into open-source statistical software R (version 3.4.1; R Core Team, 2017) for

FIGURE 1 | Schematic overview of the experimental design. For each experimental run, every DOM concentration (color gradient) was present in duplicates and randomly placed in front of the camera axis. Each flask contained a single *Daphnia magna* neonate. For details on the experimental procedure and filming regime, see the Materials and Methods section.

further analysis (Supplementary Data 3). Tracks shorter than 1 s, and shorter tracks occurring simultaneously to longer tracks were excluded to prevent false detections (e.g., mirror images of daphnids in the bottle walls or false traces) from the data.

From the position data, five behavioral traits were computed to analyse the individuals' behavior. The explored area (mm^2) is the area enclosed by the convex envelope of the coordinates and represents a measure of explorative behavior. The swimming speed ($mm\ s^{-1}$) is the average of the frame to frame distances over time. The traveled distance (mm) is the gross sum of all traveled distances and was used as a measure of general activity; as was the swimming time (%). The median of the swimming depth (mm) was taken as a measure of UV stress response (Hylander et al., 2014). While these traits can be correlated, they capture different characteristics of an individual's movement (Chapman et al., 2011; Heuschele et al., 2017).

Statistical Analyses

All statistical analyses were carried out using open-source statistical software R (version 3.4.1; R Core Team, 2017) and its add-on packages MASS (version 7.3-47; Venables and Ripley, 2002), MuMIn (version 1.15.6; Barton, 2016), and nlme (version 3.1-131; Pinheiro et al., 2016).

Each of the five behavioral traits were analyzed as independent responses in linear mixed-effects (LME) models. DOM (mg C L^{-1}), UVR (μmol $UVA_{340}\ m^{-2}\ s^{-1}$), time (h), and size of the *Daphnia* (mm) served as fixed-effect parameters, and the initial models allowed for all interactions. Each run (i.e., each round of filming) was treated as random slope, and individuals nested inside the experimental day were the grouping structure. Before analyses, the respective response variables were power-transformed to maximize log-likelihood (Box and Cox, 1964).

Parameter selection for the final model was based on the Akaike's corrected information criterion (AICc; Akaike, 1974; Burnham and Anderson, 2004). For this, the AICc of models of all possible parameter combinations were determined using maximum likelihood. All models within a Δ of 2 of the lowest AICc were updated using restricted maximum likelihood.
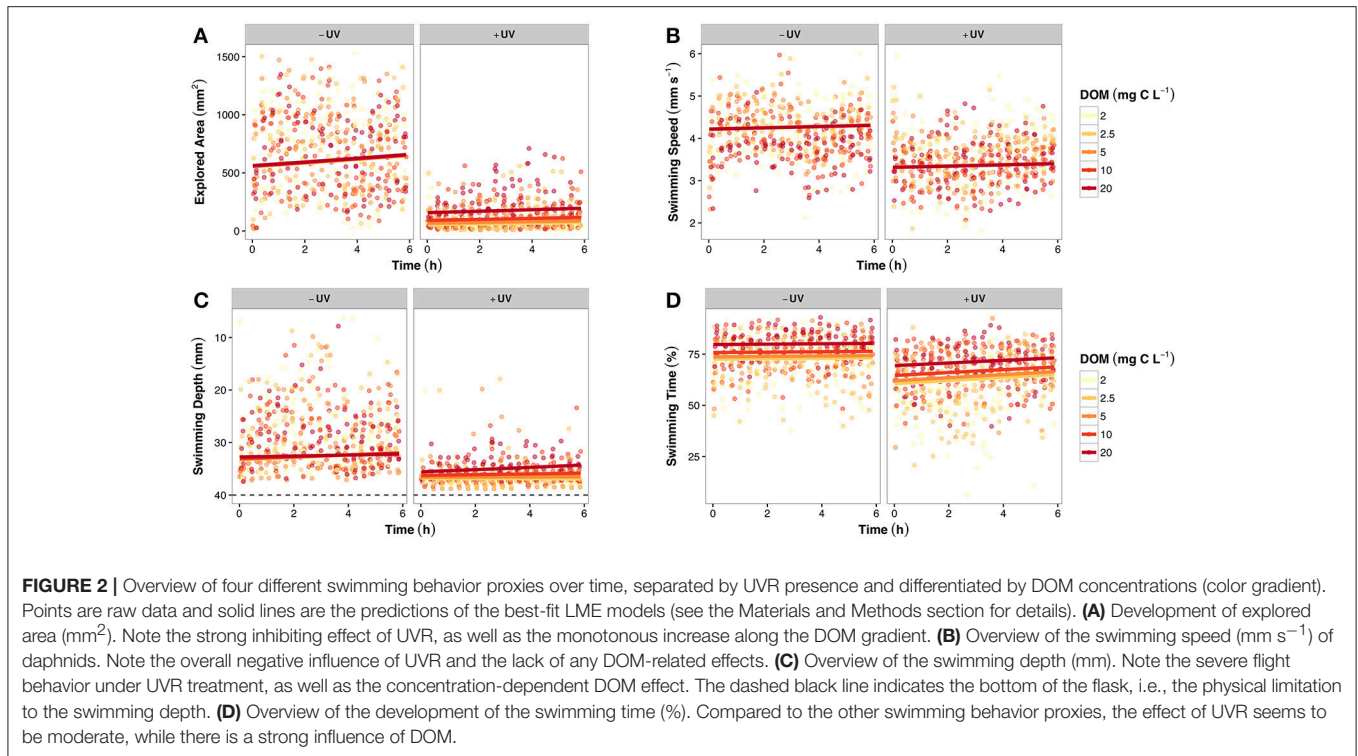
The number of models fulfilling this criterion varied between behavioral traits, as the treatments did not influence all aspects of swimming behavior equally strong. Model averaging of the full model was then used to summarize the information contained in the competing "best" models and to determine the final set of parameters (Burnham and Anderson, 2002).

After parameter selection and model averaging based on information criteria, the fixed-effect parameters of the final full models were analyzed using Wald's F-tests with marginal (type III) sum-of-squares (Pinheiro and Bates, 2000; Li and Redden, 2015), and were considered significant for $P < 0.05$. This served as proxy for the effect strength of the retained fixed-effect parameters on the swimming behavior of *D. magna*. All results are given as mean $\pm$ standard deviation. The annotated script for statistical analyses can be found in the online version of this article (Supplementary Data 4).

RESULTS

The explored area was most prominently influenced by the presence of UVR, which had an overall negative effect (**Figure 2A**). Without UVR, the explored area fluctuated between 653.7 ± 351.3 and $713.5 \pm 351.5\ mm^2$, without a clear DOM effect. In the presence of UVR, the explored area increased along the DOM gradient, from 64.7 ± 65.8 to $190.3 \pm 156.6\ mm^2$. The final LME model was averaged from two models and contained three variables with two interactions. UVR had a negative effect, and time as well as the DOM $\times$ UVR interaction had a positive effect.

The swimming speed of daphnids was mostly influenced by the presence of UVR, but apparently not by DOM (**Figure 2B**). Without UVR, the swimming speed ranged from 4.0 ± 0.6 to $4.3 \pm 0.5\ mm\ s^{-1}$; under UVR exposure, it ranged from 3.3 ± 0.4 to $3.6 \pm 0.6\ mm\ s^{-1}$. In both cases, DOM did not seem to exert an effect. The final LME model was averaged from five models and contained four parameters with three interactions. UVR had a negative effect and time a positive influence on the swimming speed.

FIGURE 2 | Overview of four different swimming behavior proxies over time, separated by UVR presence and differentiated by DOM concentrations (color gradient). Points are raw data and solid lines are the predictions of the best-fit LME models (see the Materials and Methods section for details). **(A)** Development of explored area (mm^2). Note the strong inhibiting effect of UVR, as well as the monotonous increase along the DOM gradient. **(B)** Overview of the swimming speed (mm s^{-1}) of daphnids. Note the overall negative influence of UVR and the lack of any DOM-related effects. **(C)** Overview of the swimming depth (mm). Note the severe flight behavior under UVR treatment, as well as the concentration-dependent DOM effect. The dashed black line indicates the bottom of the flask, i.e., the physical limitation to the swimming depth. **(D)** Overview of the development of the swimming time (%). Compared to the other swimming behavior proxies, the effect of UVR seems to be moderate, while there is a strong influence of DOM.

The swimming depth, again, was mostly influenced by the presence of UVR; however, a DOM-influence was visible under the UVR treatment (**Figure 2C**). Without UVR, the swimming depth ranged from 28.2 ± 7.0 to 29.9 ± 6.1 mm, while it increased along the DOM gradient from 37.4 ± 1.8 to 34.9 ± 2.1 mm under UVR exposure. The final LME model was averaged from 16 models and contained four parameters with six interactions. UVR and the UVR × time interaction increased the swimming depth, while the DOM × UVR × time triple interaction had a decreasing effect.

The traveled distance during the experiment, again, was mostly influenced by the presence of UVR, but not visibly by DOM; however, a temporal trend was observable (Supplementary Figure 2). Without UVR, the traveled distance ranged from 176.0 ± 33.9 to 195.3 ± 29.9 mm, without a clear DOM effect. Under UVR treatment, it increased along the DOM gradient from 118.3 ± 42.9 to 141.2 ± 31.1 mm. The final LME model was averaged from 11 models and had four parameters with four interactions. UVR had a negative effect, and the DOM × UVR interaction a positive effect. DOM had a positive effect and the DOM × size interaction had a negative influence.

In contrast to the previous parameters, the swimming time appeared to be mostly influenced by DOM, but also contrastingly by UVR (**Figure 2D**). Without UVR, the swimming time increased along the DOM gradient from 68.6 ± 10.9 to 80.4 ± 6.4%. The same pattern could be observed under UVR exposure, as swimming time increased from 55.0 ± 14.8 to 68.6 ± 10.0% along the DOM gradient. The final LME model was averaged from four models and contained four parameters with two interactions. DOM had a positive effect, whereas UVR had a negative influence on the swimming time. The interaction between time and UVR had a positive effect.

Details on the respective LME model parameters and parameter significances can be found in **Table 1**, and summary statistics for all endpoints and treatments are given in Supplementary Table 1.

DISCUSSION

In the present study, we demonstrate the interactive effects of DOM and UVR on zooplankton swimming behavior. For our model organism *D. magna*, DOM mostly altered swimming behavior under UVR exposure, seemingly relieving the detrimental UVR effects. Individuals explored a larger area and traveled more when "protected" from UVR. This can be interpreted as a direct effect of UVR-absorption by DOM molecules, i.e., shading.

Without UVR exposure, no differences in motility were measurable along the DOM gradient, with the exception of the swimming time (**Figure 2D**), which was positively correlated to DOM independent of UVR exposure. This indicates that DOM itself has the potential to alter zooplankton behavior. A possible explanation could be a change in water-borne oxygen concentration due to chemical consumption in oxidation processes (Asakura et al., 2010; Ylla et al., 2012).

Increased swimming activity under higher DOM levels would allow individuals to increase filter feeding. Likely, the increase in DOM-associated free nutrients (e.g., carbon, nitrogen, and phosphorus; Qualls et al., 1991; Williams and Edwards, 1993)

TABLE 1 | Overview of the results from model averaging for the five different behavioral parameters: explored area, swimming speed, swimming depth, traveled distance, and swimming time.

Parameter	Effect direction	*P*-value	Significance
EXPLORED AREA			
DOM	+	0.915	
UVR	−	<0.001	***
Time	+	0.002	**
DOM × UVR	+	0.002	**
DOM × Time	+	0.976	
SWIMMING SPEED			
DOM	−	0.901	
UVR	−	<0.001	***
Time	+	0.037	*
Size	+	0.998	
DOM × UVR	+	0.998	
DOM × Size	−	0.998	
UVR × Size	−	1.000	
SWIMMING DEPTH[†]			
DOM	−	0.678	
UVR	+	<0.001	***
Time	−	0.365	
Size	+	0.554	
DOM × UVR	−	0.320	
DOM × Time	+	0.404	
DOM × Size	+	0.754	
UVR × Time	+	0.022	*
Time × Size	+	0.653	
DOM × UVR × Time	−	0.055	.
TRAVELED DISTANCE			
DOM	+	0.088	.
UVR	−	<0.001	***
Time	−	0.266	
Size	+	0.189	
DOM × UVR	+	0.033	*
DOM × Size	−	0.089	.
UVR × Time	+	0.967	
Time × Size	+	0.183	
SWIMMING TIME			
DOM	+	<0.001	***
UVR	−	<0.001	***
Time	+	0.599	
Size	+	0.547	
DOM × Time	+	0.983	
UVR × Time	+	0.064	.

For details on the parameter selection, model averaging procedure, and significance calculations, see the Materials and Methods section. The effect direction indicates general positive or negative effects of the parameters, while the P-values indicate the effect intensity; ·P < 0.1, *P < 0.05, **P < 0.01 and ***P < 0.001. [†]Note that an increase in swimming depth (+) means that the Daphnia magna neonate is actually deeper in the water column.

would also benefit bacterial growth (Anesio et al., 2005; Buchan et al., 2014), which could increase food source availability for daphnids.

The singular effects of UVR on the swimming behavior of *Daphnia* species have repeatedly been studied elsewhere and our findings corroborate these studies. As daphnids actively recognize the presence of harmful UVR through their compound eyes (Smith and Macagno, 1990), their first initial behavioral response is the flight into deeper waters (**Figure 2C**; Leech and Williamson, 2001; Rhode et al., 2001; Fischer et al., 2006; Williamson et al., 2011). By doing so, they effectively eliminate potential metabolic harm from UVR (Häder and Sinha, 2005). If not constraint by the size of the culture flasks, the daphnids in our experiments likely would have swum several decimeters deeper (Hylander et al., 2014), until the UVR intensity was below their perception threshold. The intensity is modulated by the strong light attenuation of DOM in the UVR waveband (Thrane et al., 2014; Wolf et al., 2018), so daphnids in browner water would reside higher up in the water column in the presence of UVR. The influence of UVR on the explored area in our experiment is a direct result of this "flight" behavior, as daphnids were mostly residing in the bottom of the flask and could not swim deeper.

The decrease in swimming speed due to UVR could point toward a shift in energy allocation, from motility to oxidative stress defense and repair mechanisms. The negative UVR impact on traveled distance can be explained either as an artifact of the flask depth, or as a result of activated defense and repair mechanisms, which seemingly calm down daphnids (Hylander et al., 2014). Over time, swimming behavior generally increased, which in this context could indicate successful defense mechanisms (Rautio and Tartarotti, 2010; Lushchak, 2011).

While DOM and UVR were the dominant factors affecting swimming behavior (**Figure 2**, **Table 1**), both the duration of the experiments and size of the daphnids had some influence as well. Although the size of daphnids did not have strong effects on any observed endpoint, larger specimen seemingly covered more distance than their smaller peers. The experimental duration altered both the explored area and the swimming speed. This indicates acclimation processes of daphnids to the experimental conditions and makes a strong case for our approach of repeated measurements of activity patterns over a reasonable time scale (Hansson et al., 2016). Our approach is especially well-suited to detect sublethal effects of environmental changes on behavior, well-before detrimental physiological or genetic damages are detectable (Lima, 1998; Pan et al., 2017).

In our study, we focused on the interaction between DOM and UVR on swimming behavior. However, both factors alter several other environmental factors relevant for zooplankton fitness. In nature, most of the UVR photons will be absorbed within the first meter of the water column (Thrane et al., 2014). However, daphnids often inhabit shallow ponds, with—in extreme cases—only a few centimeters of water depth. Under these conditions, behavioral reactions alone are insufficient and additional physiological protection is needed, which comes at energetic costs (Leech et al., 2005; Wolf et al., 2017). Because of the immensely negative effects of UVR, the filtration efficiency of UVR-exposed *Daphnia* is reduced (Fernández and Rejas, 2017), which can further deplete energy reserves.

On an ecosystem level, the effects of water browning on primary production point toward a negative impact due to

increased light attenuation (Buchan et al., 2014; Kissman et al., 2017). Besides affecting physiological processes of organisms, interactions between DOM and UVR also affects species interactions in ecosystems, e.g., UVR photochemically degrades kairomones, rendering them ineffective (Sterr and Sommaruga, 2008). Water browning could thus increase the effect duration of kairomones in water. This could be beneficial for zooplankton, by prolonging alertness levels to predator presence (Hylander et al., 2009). The light regime also influences predator escape efficiency, mostly through visual predator avoidance (Brewer et al., 1999). In this case, water browning should decrease the chances of spotting a predator—or, *vice versa*, prey (Ranåker et al., 2012; Lindholm et al., 2016). In our experiments, *D. magna* individuals generally increased exploration activity with increasing DOM levels, suggesting that encounter rates with predators could increase. However, whether predator or prey will benefit from water browning will also depend on the specific combination of the visual sensitivities and reaction distances in both organisms (Utne-Palm, 2010).

In summary, we demonstrate that increased DOM can alleviate the negative effects of UVR on zooplankton swimming behavior. The multitude and complexity of pathways and interactions between DOM, UVR, and other factors makes it difficult to predict ecosystem responses. It is clear that the continued trend of water browning in freshwater systems of the Northern hemisphere will challenge biota throughout ecosystems, providing both beneficial, but also detrimental new circumstances to cope with. Besides freshwater systems, also coastal ecosystems are affected by increased water browning (Aksnes et al., 2009). Hence, our findings are likely also relevant for marine zooplankton. Given that organisms first react to changing environmental conditions by altering their behavior, our experimental approach can be used to investigate short-term effects of multiple stressors in small organisms, not only in the context of water browning, but also other environmental challenges.

AUTHOR CONTRIBUTIONS

RW conceived the study and both authors designed the experiment. JH was responsible for the technical setup and RW carried out the experiment. JH developed the movie and tracking evaluation, and both authors worked on the statistical analysis, figures, and tables. RW wrote the manuscript with input from JH.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2018.00026/full#supplementary-material

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