PRIMARY RESEARCH PAPER

Effects of dissolved organic carbon gradient on epilimnetic zooplankton communities in lakes

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Abstract Lake browning is expected to change aquatic ecosystems considerably. The changes that may occur in zooplankton communities with a high concentration of dissolved organic carbon (DOC) are little studied and not yet sufficiently understood. We studied zooplankton communities in Finland in 27 lakes with a wide DOC range. We explored how zooplankton diversity and biomass vary along a DOC gradient and how species belonging to different functional groups respond to varying DOC concentrations. The total biomass of zooplankton was not related to DOC concentration, but diversity decreased and the negative linear trend in diversity coincided with an increase in omnivorous zooplankton taxa, whereas several other herbivorous zooplankton taxa were displaced from the community along the gradient of DOC. The results of our study suggest that some well-adapted taxa, especially omnivorous taxa, can benefit from lake browning, but a larger number of taxa suffer from unfavourable conditions caused by high DOC concentration. DOC-induced changes in predation pressure and changes in phytoplankton community in terms of resource availability for zooplankton should be emphasized in future research to understand the effects of lake browning on zooplankton.

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Introduction

In temperate and boreal regions, lakes have experienced a gradual and long-term increase in water colour (e.g. Monteith et al., 2007; Clark et al., 2010). The browning of lakes has been suggested to be caused by many factors, such as climate warming, increased precipitation and decreased atmospheric sulphate deposition (Evans et al., 2005; Weyhenmeyer & Karlsson, 2009). Regardless of the causes, browning is generally linked to increased leaching of terrestrial dissolved organic carbon (DOC) to aquatic ecosystems. Increasing DOC concentrations in lakes can have considerable consequences for ecosystem structure and function (Brothers et al., 2014; Solomon et al., 2015) and interfere with different kinds of human water use, for example, recreation, fisheries and drinking water supply (Lavonen et al., 2013). The consequences of lake browning are complex because

increasing DOC content alters the physical and chemical environment of lakes, which further affect organisms and these changes cascade and interact with each other (Brothers et al., 2014).

For instance, lake surface water warming is determined primarily by rising air temperatures (Schmid et al., 2014), but water transparency also regulates the absorption of solar radiation in the water column (Read & Rose, 2013). Consequently, lake browning and rising temperatures have led in more profound thermal stratification and bottom water anoxia in lakes (Jankowski et al., 2006). Light and temperature are the main regulating factors in lakes because they control primary production, biochemistry and habitat suitability for many organisms (MacIntyre et al., 2006). These changes in light and heat could result in less biomass production of primary producers, ultimately affecting consumers like zooplankton and fish and thus the biodiversity of freshwater ecosystems (Solomon et al., 2015). Overall, the effects of browning on lake productivity and food web structure have been extensively studied and discussed, but the conclusions remain uncertain due to the complex effects of browning (Creed et al., 2018 and references therein).

Zooplankton play an important link in lake food webs between the primary producers and other consumers such as fish (Ask et al., 2009; Estlander et al., 2010). The effects of lake browning on zooplankton communities, or on specific taxa, are not consistent and well-documented since several DOC-related factors can affect zooplankton both directly and indirectly. The negative impacts of lake browning are usually related to the deterioration of the resource quality and habitat availability. For example, Kelly et al. (2014) showed a strong negative relationship between zooplankton production and water transparency and suggested that the relationship was mainly due to habitat loss and poor total organic carbon (TOC) quality for zooplankton. On the other hand, DOC can enhance both visual (water colour) and physiological (low oxygen concentration in the hypolimnion) refuges in which zooplankton can avoid fish predation (Estlander et al., 2009, 2010), thus resulting in a larger individual size of cladocerans (Estlander et al., 2009) when food resources are not limited.

DOC may limit primary production via strong light extinction (e.g. Carpenter et al., 1998), but it can also provide resources for zooplankton by increasing bacterial productivity (Lennon & Pfaff, 2005). In addition, nutrients (nitrogen and phosphorus) are commonly co-transported with DOC (e.g. Jones et al., 2012), which stimulates the abundance of phytoplankton and further herbivorous zooplankton (McQueen et al., 1986). In addition, increasing levels of nutrients also affect nutrient stoichiometry (Bergström & Karlsson, 2019), which affects the quantity and quality (e.g. Isles et al., 2020) of zooplankton food resources. According to Solomon et al. (2015), the effects of DOC concentration on many processes in lakes are non-linear, and they suggest a DOC concentration threshold from 10 to 14 mg l^{-1} above which, e.g. the primary production is greatly reduced. For example, a moderate level of DOC can increase primary production by providing energy and nutrients to phytoplankton (Klug, 2002), but when the DOC concentration exceeds a certain threshold the low light starts to limit primary production (Ask et al., 2009). Referring to this, only a few studies have focused on lakes in which the potential threshold concentration was exceeded (Craig et al., 2015). Thus, the zooplankton community changes that may take place with a high concentration of DOC are rarely studied and not yet sufficiently understood in lakes.

In addition to nutrients, other browning-related changes in the environment may impact zooplankton community groups differently due to taxon-specific tolerance to environmental conditions such as oxygen depletion and food shortage (Jones et al., 2012; Karpowicz & Ejsmont-Karabin, 2018); thus, the environmental changes can be reflected in different and complex ways in zooplankton diversity and biomass. For example, many rotifer taxa are less dependent on autotrophic production than crustacean zooplankton (Ruttner-Kolisko, 1974); thus, an increase in DOC concentration may benefit them more than crustaceans.

Here we compare how zooplankton diversity and biomass vary across gradients in lake DOC. Especially in DOC-rich lakes, the living conditions for zooplankton are mainly restricted to the epilimnion, because DOC concentration has a strong effect on thermal stratification and vertical oxygen profiles (Jankowski et al., 2006) and anoxic conditions limit the biomass and diversity of zooplankton (Karpowicz & Ejsmont-Karabin, 2018; Karpowicz et al., 2020). Previous studies have also shown that in the study area, zooplankton in lakes is concentrated in the

epilimnion during thermal stratification in the summer (Estlander et al., 2009, 2010; Rask et al., 2014). Therefore, to compare the zooplankton communities between lakes, where the environmental conditions are very different, our study focused on epilimnetic zooplankton in the pelagic zone. Since zooplankton exploit diverse food resources and browning has been shown to increase the reliance of zooplankton on a heterotrophic microbial diet (Strandberg et al., 2023), we also assessed how species differ ecologically along the DOC gradient by studying the functional feeding habits (herbivore, carnivorous or omnivore) of zooplankton.

As primary consumers, we expected that zooplankton biomass would follow a similar, unimodal pattern in terms of DOC concentration as that of primary producers in previous studies (Solomon et al., 2015; Kelly et al., 2018; Horppila et al., 2023). Regarding the diversity of zooplankton, we expected that increasing DOC concentration would reduce overall biodiversity due to habitat loss that may amplify competitive interactions amongst different zooplankton taxa, since niches are few in highly humic lakes because of the shallow epilimnion and oxygen depletion in the hypolimnion. We also hypothesized that increasing DOC concentration in lakes would favour carnivorous and omnivorous over herbivorous feeding habits of zooplankton communities, as Strandberg et al. (2023) showed that zooplankton would increasingly be supported by a heterotrophic microbial diet when the DOC concentration increases. To test these hypotheses, we analysed epilimnetic zooplankton and water quality data from lakes in Finland with a comprehensive gradient of DOC and nutrient concentrations.

Materials and methods

Field sampling

The study was conducted in 27 lakes in western and southern Finland during the peak of summer thermal stratification in 2019–2020. Each lake was sampled once and all lakes were sampled within two weeks in July. Three replicate zooplankton and water quality samples for physical and chemical analyses were taken close to the deepest point of each from the epilimnion lake using a 50 μm mesh plankton net

(25 cm opening) at 0.5 m s^{-1} to reduce the escapement of zooplankton (Estlander et al., 2017) and a Limnos tube sampler (volume 2.8 l) for water samples. Zooplankton samples were taken from each metre of the epilimnion after estimating the depth of the thermocline and preserved in 4% formaldehyde in the field.

From the water quality samples, total P (TP), total N (TN), iron (Fe), DOC, water colour and chlorophyll *a* were determined in the laboratory. TP and TN concentrations were determined from the samples with a Lachat autoanalyser (QuickChem Series 8000 m, Lachat Instruments, Hach Co., Loveland, CO, USA) and DOC concentration with a Shimadzu TOC 5000A analyser according to the standard SFS-EN 1484 (Finnish Standards Association, 1997). Fe was analysed using an atomic absorption spectrophotometer (Varian SpectrAA 220FS, Varian, Palo Alto, CA) following the standard SFS 3044 (Finnish Standards Association, 1980). Chlorophyll-*a* concentration was analysed after filtration on Whatman GF/C filters and extraction with ethanol with a Hitachi F-4000 (Hitachi, Japan) fluorescence spectrophotometer with excitation and emission wavelengths of 435 and 671 nm. Water colour was determined with a Shimadzu UV-1800 spectrophotometer as the absorbance of light at the 410 nm wavelength and converted to mg Pt l^{-1} following the standard SFS-EN ISO 7887 (Finnish Standards Association, 2011).

Vertical profiles of water pH, temperature and dissolved oxygen were determined in situ with a YSI 6820 CTD sonde (YSI Incorporated, Yellow Springs, Ohio). The vertical variation of light intensity in the water column was measured with a LI-1400 data logger equipped with an LI-192SA quantum sensor (LI-COR Biosciences, Lincoln, NE, USA). The light extinction coefficient (K_d) was calculated for each lake with the equation (e.g. Scheffer, 1998) $K_d = (lnI_0/I_z)/Z$, where I_0 and I_Z are the light intensities just below the surface and at depth Z. To estimate the suitable habitat availability for zooplankton, mean epilimnion depth (Z_{mix}) in each lake was determined as the layer above the depth with maximum temperature change (Keller et al., 2006).

Zooplankton analysis

In the laboratory, zooplankton were counted, their length and width (for rotifers) measured under an

inverted microscope and they were identified to species level. From each species, 30 individuals were measured to estimate the carbon biomass using species-specific carbon regressions (Bottrell et al., 1976; Vasama & Kankaala, 1990; Luokkanen, 1995). To control sample size effects on biodiversity measures (Gotelli & Colwell, 2001), we plotted the volume of analysed samples against the accumulated number of species and found that a sample size of 100 l was needed to reach stabilization of the accumulation curve. Therefore, parallel zooplankton samples were pooled for calculating species richness and diversity. Zooplankton species diversity was determined using the Shannon–Weaver diversity index (H′): H′ = $\sum pi$lnpi, where pi is the proportion of species i in the sample (Shannon & Weaver, 1949). A high value of H′ suggests a diverse and equally distributed community and lower values represent a less diverse community. Zooplankton taxa were categorized into the herbivore, omnivore and carnivore categories (supplementary information (SI) 1) according to their predominant feeding habits (Papirńska, 1985; Kling et al., 1992; Šorf & Brandl, 2012; Barnett et al., 2007; Gilbert, 2022) and the species richness and biomass of each category were calculated for analysis.

Data analysis

The statistical analyses were performed using IBM SPSS Statistics for Windows, version 21.0 (IBM Corp., Armonk, NY, USA). First, Pearson correlations were run between physico-chemical parameters to distinguish key abiotic variables related to DOC concentration. The effects of DOC and chlorophyll-a concentration on zooplankton species richness, H′ and biomass in the study lakes were studied with stepwise multiple linear regressions. Variables were selected in the multiple regression only if $P < 0.05$. Before the regression analyses, data were ln-transformed to improve normality and the potential collinearity of the independent variables was tested. All analyses were performed both for the entire zooplankton community but also separately for different feeding categories (herbivore, omnivore and carnivore). Because previous studies on primary producers predict a curvilinear, unimodal relationship with DOC concentration (e.g. Kelly et al., 2018; Horppila et al., 2023), quadratic regression was applied to chlorophyll-a and zooplankton biomass in relation to DOC concentration.
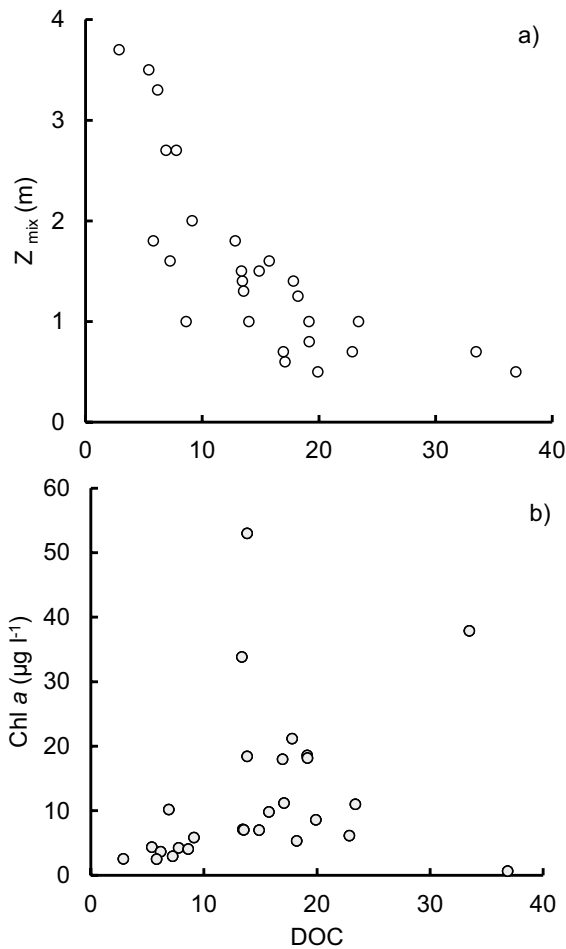
Results

Environmental parameters

The water quality varied widely amongst the study lakes (Table 1). The Z_{mix} varied from 0.5 to 3.7 m and Secchi disc depth from 0.25 to 4.5 m. The average temperature in the epilimnion varied from 20 to 23 °C and the oxygen concentration from 6.1 to 10.3 mg l^{-1}. The DOC concentration varied from 2.9 to 36.9 mg l^{-1}, TP from 5 to 61 µg l^{-1}, TN from 197 to 1147 µg l^{-1} and the chlorophyll-a concentration from 0.6 to 53 mg l^{-1} (Table 1). The DOC concentration showed a strong negative relationship with Z_{mix} ($r = -0.75$, $P < 0.01$) (Fig. 1a) but correlated positively with K_d ($r = 0.86$, $P < 0.01$), TP ($r = 0.58$, $P < 0.01$), TN ($r = 0.72$, $P < 0.01$) and Fe ($r = 0.59$, $P < 0.01$). Chlorophyll a (Chl-a) increased slightly with DOC concentration, but the correlation was not significant, as Chl-a showed no linear relationship with DOC concentration (Fig. 1b). However, Chl-a showed unimodal variation with DOC concentration (Fig. 1b). The relationship between the chlorophyll-a concentration of the lakes and DOC was defined by a second-order polynomial function log(Chl a) = $-0.019 + 0.126 \times DOC - 0.003 \times DOC^2$ ($F_{2,24} = 18.83$, $R^2 = 0.578$, $P < 0.001$).

Species richness and diversity

A total of 46 species (30 rotifer, 11 Cladocera, 5 Copepoda) were found in the studied lakes (SI1). The most abundant species was rotifer *Keratella cochlearis* (Gosse, 1851), which was found in all lakes studied. The other typical rotifer species were *Polyarthra remata* Skorikov, 1896 (25 lakes), *Kellicottia longispina* (Kellicott, 1879) (24 lakes) and *Ascomorpha saltans* Bartsch, 1870 (23 lakes). The most abundant crustacean species were *Mesocyclops leuckarti* (Claus, 1857) (25 lakes), *Bosmina longirostris* (O.F.Müller, 1776) (22 lakes) and *Eudiaptomus gracilis* (Sars G.O., 1863) (19 lakes). Certain taxa, such as herbivorous *Collotheca* sp., *Euchlanis* sp., *Filinia* sp., *Gastropus stylifer* Imhof, 1891, *Pompholyx* sp. and *Holopedium gibberum* Zaddach, 1855 were

Table 1 Main characteristics of the 27 studied lakes in southern and western Finland. Chemical variables represent values for the epilimnion

Lake	Surface area (ha)	Maximum depth (m)	Z_{mix} (m)	Secchi depth (cm)	Dissolved organic carbon mg l^{-1}	Iron mg l^{-1}	pH	Total phosphorus µg l^{-1}	Total nitrogen µg l^{-1}	Chl a µg l^{-1}
Syrjänalunen	1.0	9	3.7	400	2.9	0.1	5.7	7	197	2.5
Valkea Mustajärvi	13.1	10	3.5	450	5.4	<0.1	7.5	9	370	4.3
Vähäjärvi	7.9	10	1.8	350	5.8	0.2	5.6	9	353	2.5
Selkjärvi	22.7	10	3.3	290	6.2	0.2	5.6	10	330	3.7
Harjulampi	1.1	10	2.7	130	6.9	0.2	5.3	18	394	10.2
Iso Valkjärvi	3.8	8	1.6	140	7.3	0.1	5.7	18	430	3.0
Mustajärvi	165.9	7	2.7	240	7.8	0.2	6.5	5	272	4.3
Hokajärvi	8.4	5	1.0	180	8.6	0.8	6.0	9	337	4.0
Isojärvi	265.0	8	2.0	250	9.1	0.2	6.3	16	527	5.8
Kernaalanjärvi	444.8	8	1.8	70	12.8	0.6	10.3	61	737	53.0
Neva-Lyly	10.7	5	1.5	75	13.4	0.2	6.0	21	453	33.8
Iso Särkijärvi	15.7	4	1.4	100	13.5	1.6	6.1	14	388	7.1
Pitkäniemenjärvi	13.9	9	1.3	110	13.6	0.6	6.5	15	457	7.0
Kangaslammit	11.4	3	1.0	45	14.0	0.5	4.6	21	447	18.4
Vähä Särkijärvi	12.2	4	1.5	140	14.9	0.6	6.4	14	373	7.0
Rahtijärvi	12.0	10	1.6	115	15.8	0.5	6.4	19	547	9.8
Iso Koura	17.3	3	0.7	60	17.0	1.2	5.8	24	509	18.0
Alkkianlampi	8.2	3	0.6	50	17.1	1.4	6.0	28	448	11.2
Kyynäröjärvi	24.6	3	1.4	55	17.8	1.3	6.8	61	1057	21.2
Alempi Rajajärvi	2.8	4	1.3	70	18.2	0.6	5.2	18	540	5.3
Pirttijärvi	78.7	3	1.0	60	19.2	1.3	5.9	22	515	18.6
Kärppäjärvi	19.6	3	0.8	35	19.2	3.5	6.5	33	488	18.2
Haukijärvi	2.2	7	0.5	65	19.9	1.3	5.8	18	550	8.6
Horkkajärvi	1.2	5	0.7	75	22.9	0.4	5.4	17	580	6.1
Majajärvi	3.4	12	1.0	70	23.5	0.5	5.6	33	710	11.0
Käkilammi	9.9	3	0.7	60	33.5	1.0	6.2	47	1147	37.9
Kangas-Lyly	4.3	3	0.5	25	36.9	2.5	5.1	40	690	0.6

Fig. 1 Relationship between epilimnion depth (Z_{mix}) and dissolved organic carbon (DOC) (**a**) and between chlorophyll-*a* concentration (Chl *a*) and DOC (**b**)

completely absent from the samples when the DOC concentration exceeded 20 mg l^{-1}. Overall, in several lakes only 2–3 small rotifer species dominated and accounted for 90% of the zooplankton density, whilst other taxa were sparse. Species richness varied from 12 to 21 in the studied lakes. The highest number of species (species richness 21) was detected in Lakes Kyynäröjärvi and Rahtijärvi and the lowest (species richness 12) in Lake Iso Koura.

The species richness increased with Z_{mix} and, according to the regression, Z_{mix} explained 32% ($F_{1,25} = 13.27$, $P < 0.01$) of the variation in species richness (Fig. 2a). When considering only the richness of herbivorous taxa, the DOC concentration alone explained 68% ($F_{1,25} = 56.72$, $P < 0.01$) of the

species variation. The richness of herbivorous taxa decreased considerably towards higher DOC concentrations (Fig. 2b). However, DOC concentration was positively related to the species richness of omnivorous taxa (Fig. 2b) ($R^2 = 0.36$, $F_{1,25} = 15.45$, $P < 0.01$). When Z_{mix} was added as a predictive variable together with DOC, it considerably increased the R^2 value ($R^2 = 0.47$, $F_{2,24} = 12.74$, $P < 0.01$); thus, DOC and Z_{mix} together explained 47% of the variation in richness of omnivorous taxa. Even though DOC and Z_{mix} were correlated (Fig. 1a), the collinearity statistic indicated only moderate correlation between DOC and Z_{mix} (Variance Inflation Factor (VIF) < 2.3) in the regression analysis. No consistent relationship between Z_{mix}, DOC or chlorophyll *a* and richness of carnivorous taxa was found, since only 1–2 carnivorous species (*Polyphemus pediculus* (Linnaeus, 1761) and *Leptodora kindti* (Focke, 1844)) were found from the samples (SI1). According to the regression model, Z_{mix} and chlorophyll *a* had no significant effect on zooplankton H′, but DOC alone explained 44% of the variation ($R^2 = 0.44$, $F_{1,25} = 21.54$, $P < 0.01$), which decreased towards higher DOC concentrations (Fig. 3).

Biomass

The total zooplankton biomass variation between the lakes was large: from 1 to 790 μg C l^{-1}, but the variation within the lakes was small or moderate (< 2 standard deviation from the mean biomass) with two exceptions, where the standard deviation from mean biomass was slightly higher (2.1–2.2). The biomass of herbivorous zooplankton ranged from 0.1 to 210 μg C l^{-1}, of omnivorous taxa from 0.6 to 600 μg C l^{-1} and of carnivorous taxa from > 0.1 to 70 μg C l^{-1}. The highest biomass was observed in lakes with relatively high DOC (18–24 mg l^{-1}) and the total biomass of zooplankton was determined mainly by crustaceans. Carnivorous cladocerans *Polyphemus* and *Leptodora* were relatively common in lakes with high zooplankton biomass overall, but DOC, Z_{mix} and chlorophyll *a* had no effect on their relative share of the total biomass. However, the relative share of herbivorous plankton biomass decreased whilst the biomass share of omnivores increased significantly ($R^2 = 0.24$, $F_{1,79} = 26.76$, $P < 0.01$) as the DOC concentration increased in the studied
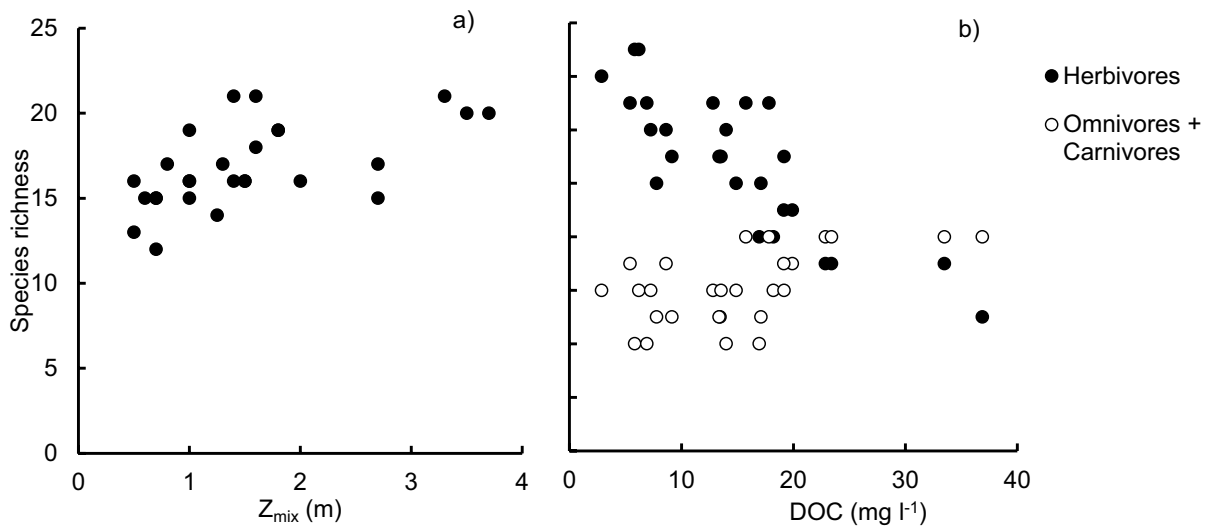
Fig. 2 Relationship between epilimnion depth (Z_{mix}) and species richness of zooplankton overall (**a**) and between the dissolved organic carbon (DOC) and richness of herbivorous (black circles) and omnivorous + carnivorous (white circles) zooplankton taxa (**b**) in the studied lakes
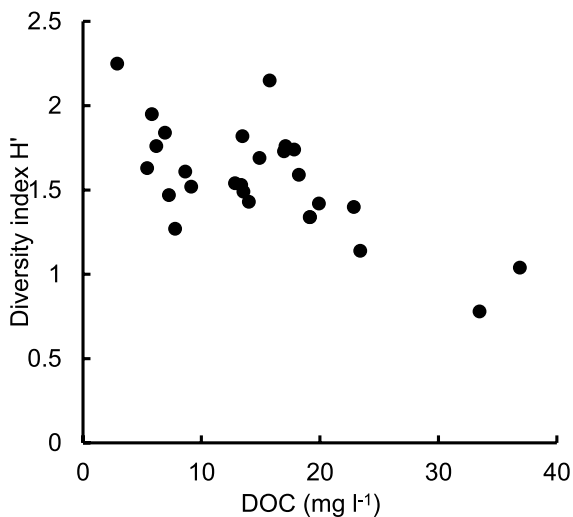
Fig. 3 Relationship between dissolved organic carbon (DOC) and the Shannon–Weaver diversity index (H′)

lakes (Fig. 4). Multiple regression analyses or quadratic regression showed no consistent relationship between Z_{mix}, DOC or chlorophyll-*a* and zooplankton biomass.

Discussion

The results of this study showed interesting patterns in the zooplankton community in relation to the DOC gradient of lakes, but not all results were consistent with the hypotheses. The total biomass of zooplankton was not related to the DOC concentration as expected, but the diversity decreased and the omnivorous taxa increased with DOC concentration. These findings indicate that some well-adapted, especially omnivorous taxa can benefit from lake browning, but a large number of taxa suffer from unfavourable conditions caused by high DOC concentration.

Biomass and non-linearity

We found a non-linear, unimodal relationship between chlorophyll *a* and DOC concentration, suggesting that when the DOC concentration exceeds ~ 17 mg l^{-1} the lack of light is likely to begin to limit phytoplankton, since the nutrients (TP and TN) showed a positive correlation with DOC. This suggests that light was the limiting factor rather than nutrients when DOC exceeded the threshold value. The pattern was similar to that presented in previous studies (Solomon et al., 2015; Horppila et al., 2023), which also suggests that radical changes may occur in lake ecosystems above a certain threshold of DOC concentration (Solomon
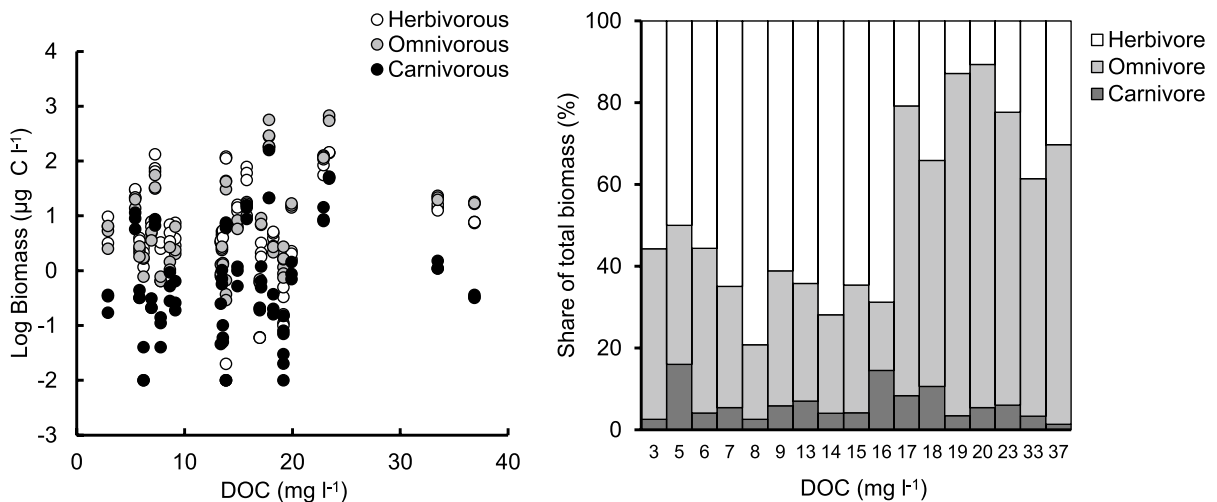
Fig. 4 The percentage composition of feeding categories (herbivorous, omnivorous and carnivorous) in zooplankton biomass in relation to DOC concentration of the studied lakes

et al., 2015). However, the zooplankton biomass did not follow this pattern but showed wide variation between lakes. DOC may provide an energy source that fuels the microbial food web (Sanders et al., 2015), which further stimulates the higher trophic levels of the food web such as the large crustaceans (Nevalainen & Luoto, 2013). The importance of bacterial production for higher trophic levels is shown in many studies and, according to Hessen et al. (1990), zooplankton production can be higher in dystrophic lakes than would be expected based on primary production. When considering the relative share of herbivores and omnivores in the zooplankton biomass, the relative share of herbivorous zooplankton biomass decreased whilst omnivorous biomass increased with DOC concentration, a pattern similar to the one we found in the species richness of zooplankton. This indicates that chlorophyll-*a* concentration provides only a rough estimate of the food resources for zooplankton in the studied lakes and does not indicate, for example, the quality of the food. For instance, some of the phytoplankton can be inedible for most of the zooplankton taxa, such as large-sized freshwater flagellated microalga *Gonyostomum semen* (Ehrenberg), which is abundant in brown lakes with high DOC concentrations (Burns, 1968; Lepistö et al., 1994; Lebret et al., 2018) and also observed in earlier studies in the studied lakes as well (Estlander et al., 2009). As mentioned earlier, mixotrophic algae that

become dominant as the DOC concentration increases can also be inedible for most of the zooplankton taxa, and some phytoplankton can even be toxic to zooplankton (Vad et al., 2021). The increase in the share of omnivorous zooplankton biomass (copepods), as well as the increase in nutrients with DOC concentration, indicate that the available food resources may favour copepods at the highest DOC concentrations (Jones et al., 2012). However, the density and composition of the different phytoplankton species must be taken into account in further studies to comprehensively assess its effects as a food resource for zooplankton in different DOC concentrations.

In addition to interspecific competition and food quality, predation is also an important factor that may regulate the biomass of zooplankton (e.g. Estlander et al., 2009). For example, high water colour impairs planktivorous fish feeding efficiency (Vinyard & O'Brien, 1976), leading to larger zooplankton individuals in high-colour lakes than in lakes with low water colour (Estlander et al., 2009). Increasing DOC concentration decreased the thickness of the epilimnion in the study lakes, which in turn may favour invertebrate predators whose predation efficiency does not depend on visibility (Giguère, 1980). Thus, high DOC concentration may induce a shift from a dominance of vertebrate predators to invertebrate predators (Liljendahl-Nurminen et al., 2003), and such a change in the

predator dominance can be reflected in the whole food web (e.g. Lampert & Sommer, 2007). When invertebrates instead of fish are the main zooplanktivores, the effect of zooplanktivory, for instance, may not cascade to primary producers as predicted by the trophic cascade hypothesis (Carpenter et al., 1985).

Species richness and diversity

In the studied lakes, the species richness of zooplankton was somewhat low but was in line with the results of Karpowicz & Ejsmont-Karabin (2021) in Polish dystrophic lakes. In addition, the species composition of zooplankton in our studied lakes, such as rotifers *K. cochlearis* and *Polyarthra vulgaris*, and crustaceans *Bosmina*, *Ceriodaphnia*, *Eudiaptomus* and *Mesocyclops*, amongst the dominant species, resembles the species structure of dystrophic lakes described in other studies (Sarvala et al., 1999; Karpowicz & Ejsmont-Karabin, 2021). In addition, Bogdan & Gilbert (1987) suggested that many of these dominant species can effectively utilize a wide food-size spectrum. Our results are also in line with those of Gannon & Stemberger (1978) and Mäemets (1983), in which rotifer taxa *Anuraeopsis*, *Pompholyx* and *Filinia* indicate eutrophic conditions, as these taxa were abundant in the lakes with highest TP and chlorophyll-*a* concentration but rare or absent in lakes with high (> 20 µg l^{-1}) DOC concentration. In addition, herbivorous rotifer taxa such as *Cephalodella*, *Euchlanis* and *Synchaeta* were rare or absent as DOC concentration increased (> 15 mg l^{-1}). These results can be due to changes in the resource supply in terms of both food quantity and quality for herbivorous zooplankton. For example, Urrutia-Cordero et al. (2017) showed that lake browning led to the dominance of mixotrophic algae in the phytoplankton community, which reduced phytoplankton diversity. The role of mixotrophic phytoplankton as food for zooplankton is, however, unclear. Vad et al. (2021) suggested both beneficial and adverse effects on *Daphnia*, depending on, for example, the species-specific differences in toxicity.

Whilst the number of herbivorous rotifer taxa declined with increasing DOC concentration, omnivorous *Asplanchna* and *Ploesoma* became more common. According to Gilbert (2022), *Asplanchna* and *Ploesoma* are omnivores/predators

that can prey on several rotifer taxa and even small crustaceans. Correspondingly, the abundance of omnivorous copepods, which have also been shown to prey on rotifers (Brandl, 2005), increased with DOC concentration. The increase in DOC concentration in the lakes thus seemed to increase the predation pressure on the rotifer community when the depth of the epilimnion decreased, which was a significant explanatory factor for the decrease in the general species richness of zooplankton. This may indicate that DOC regulates light-related habitat and resource variables, leading to habitat loss and/or increasing interspecific competition in (herbivorous) zooplankton sharing limited, and potentially low quality, resources when the DOC concentration increases (Karpowicz & Ejsmont-Karabin, 2018; Vad et al., 2021). Consequently, habitat loss and changes in food quality, together with potentially increased predation pressure by rotifers and copepods with increasing DOC concentration, may explain the decrease in overall species richness in the studied lakes.

Although the number of omnivorous taxa increased with DOC concentration, the diversity of zooplankton was negatively related to DOC. Thus, the abundance of omnivorous taxa did not increase enough to compensate for the decrease in herbivorous taxa. Our results are in line with Robidoux et al. (2015), who found a similar declining pattern in zooplankton diversity when the DOC concentration increased. The relatively distinct linear decrease in zooplankton diversity with increasing DOC concentration was somewhat unexpected, since DOC can increase bacterial productivity (Lennon & Pfaff, 2005) and thus provide enough resources for zooplankton. Indeed, increasing DOC concentration seemed to benefit omnivorous taxa, suggesting that the zooplankton community became less dependent on primary production as DOC concentration increased. In addition, variations in the DOC:nutrient ratios, which affect both the quantity and quality of zooplankton food resources (Isles et al., 2020), may favour certain species with high growth rates.

It is commonly known that, for example, temperature and oxygen gradients become steeper as DOC increases in lakes (Jankowski et al., 2006). As a result, living conditions may become too challenging for certain zooplankton species (Karpowicz & Ejsmont-Karabin, 2018). High environmental variability

usually leads a large number of adapted organisms able to tolerate varying conditions, but low biodiversity overall (McLusky & Elliott, 2007). Here, this was shown as a strong dominance of a few species in many lakes where only a couple of species accounted for most of the zooplankton density. For instance, zooplankton taxa can show divergent responses to DOC concentration, from beneficial to deleterious.

The data did not account for possible vertical migrations of zooplankton or predators of zooplankton, or the seasonal dynamics of zooplankton communities. Consequently, we compared the effects of DOC-related factors on the between-lake variation rather than the seasonal variation of zooplankton. However, we sampled all the 27 lakes within 14 days during the peak occurrence of zooplankton in Finland (Estlander et al., 2009, 2010), to minimize the effect of seasonal variation on our results. In addition, it has been shown that the vertical migration of zooplankton is more intense and more likely to take place in lakes with high water transparency (Dodson, 1990). Accordingly, the decline in zooplankton diversity in relation to DOC should have been even steeper if vertical migration had considerably affected the results.

Conclusions

In conclusion, we show that the effects of DOC can vary notably between closely related species, with favourable or adverse consequences for zooplankton. Increasing DOC concentration in lakes can result in a gradual decrease in zooplankton diversity. The negative linear trend in diversity coincided with an increase in omnivorous zooplankton taxa, whereas several other herbivorous zooplankton taxa declined from the community with intensifying DOC gradient. Our data suggest that DOC regulates the light-driven factors in lakes, with consequent impacts on food quality and habitat availability for zooplankton, which is reflected in the diversity, biomass and functional feeding habits of the zooplankton community. DOC-induced changes in predation pressure and changes in the phytoplankton community in terms of resource availability for zooplankton should be emphasized in future research to understand the effects of lake browning on zooplankton.

Data availability Data are available from the authors upon reasonable request.

Declarations

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