Canadian Journal of
Fisheries and
Aquatic Sciences

OPEN ACCESS | Research Article

Dissolved organic carbon suppresses benthivorous fish biomass by mediating invertebrate resources

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Abstract

Benthic invertebrates and benthivorous White Sucker (*Catostomus commersonii*) were surveyed in eight stratified boreal lakes with DOC concentrations ranging from 3.5 to 9.2 mg· L^{-1} at the IISD Experimental Lakes Area (IISD ELA) in northwestern Ontario, Canada. Chironomids dominated benthic invertebrate biomass and White Sucker was the dominant fish species. Both White Sucker biomass-catch-per-unit-effort (BPUE) and chironomid biomass were positively correlated with mean light irradiance. Higher biomasses of fish and chironomids occurred in lakes with a higher proportion of their volume in the photic zone, which was a function of both DOC concentrations and lake basin morphometry. White Sucker BPUE was also strongly positively correlated with chironomid biomass. A mixing model using stable isotopes indicated that allochthony increased with DOC for both littoral benthic invertebrates and White Sucker. Greater allochthony was also correlated with lower invertebrate biomass and White Sucker BPUE. Our results suggest that DOC suppresses benthivorous fish by reducing the availability of critical food resources. Chironomid biomass appears to decrease with DOC because of lower light penetration that potentially affects primary productivity and the quality of their food resources.

Key words: Catostomidae, macroinvertebrates, stable isotopes, allochthony, DOC, light

Introduction

Concentrations of dissolved organic carbon (DOC) are increasing in lakes and rivers of the northern hemisphere, coincident with changes in temperature, hydrological processes, land use, water management, and reductions in acid deposition (de Wit et al. 2021). Terrestrial inputs account for up to 95% of the DOC pool of lakes (Wilkinson et al. 2013) and have been shown to influence the productivity of all lake trophic levels, from primary producers to fish (Solomon et al. 2015; Creed et al. 2018). In boreal lakes, high concentrations of terrestrial DOC may shade the water column, altering the vertical distribution of light, heat, oxygen and nutrients (Solomon et al. 2015; Creed et al. 2018). DOC-mediated effects on light availability can suppress benthic and pelagic primary production (Ask et al. 2009; Godwin et al. 2014), which in turn can limit resources for invertebrates that are key dietary items for many fish species (Karlsson et al. 2009; Stasko et al. 2012). Higher DOC concentrations may also decrease the foraging efficiency of visual predators, such as fish (Stasko et al. 2012; Solomon et al. 2015).

DOC may also affect habitat availability for consumers through its effects on dissolved oxygen (DO) and temperature (Jane et al. 2024). Terrestrial DOC absorbs light, concentrating heat at the lake surface, resulting in shallower, more stable epilimnia (reviewed by Creed et al. 2018). As a result, a greater proportion of lake volume and sediment area may fall within the hypolimnion, where temperatures are lower, and water is isolated from atmospheric exchange. In lakes with high DOC concentrations, loss of optimal oxy-thermal habitat volume for brook trout is likely to occur more frequently (Jane et al. 2024) and benthic invertebrate productivity may be supressed due to a reduction in oxygenated habitat (Craig et al. 2015).

Food web tracers such as stable isotopes and fatty acids indicate that fish utilize terrestrial organic matter both directly and indirectly as a resource and that relative utilization of carbon derived from terrestrial sources increases with DOC concentrations (Solomon et al. 2011; Karlsson et al. 2015). Despite these findings, it remains unclear whether increased terrestrial organic matter can compensate for coincident decreases in autochthonous primary production due to light attenuation. Terrestrial organic matter is often considered a low-quality resource for invertebrate and fish consumers, in part because it lacks essential fatty acids, and has a lower trophic transfer efficiency (Berglund et al. 2007; Brett et al. 2009). Increased utilization of terrestrial organic matter has been found to be associated with decreased biomass production in zooplankton and fish (e.g., Kelly et al. 2014; Karlsson et al. 2015; Tonin et al. 2022), and others have observed lower fish biomass and growth rates with increasing DOC concentrations (Benoit et al. 2016; Craig et al. 2017; Seekell et al. 2018). In contrast, there is also evidence that inputs of terrestrial DOC can directly subsidize lake food webs and increase nutrient availability, which, in turn, may enhance primary production (reviewed by Creed et al. 2018).

The objective of our study was to investigate how the biomass and trophic relationships of invertebrates and a common benthivorous fish, White Sucker (*Catostomus commersonii*), varied with DOC concentration. We used a survey of eight stratified boreal lakes to investigate relationships between DOC concentrations and the biomass of White Sucker and their invertebrate prey. Using stable isotopes of hydrogen (H), carbon (C), and nitrogen (N) with a three-isotope Bayesian mixing model, we examined how basal resource use by White Sucker and invertebrates varied with DOC concentrations. This included determining whether utilization of C derived from terrestrial organic matter (allochthony) by White Sucker and invertebrates increased with DOC concentration, potentially acting as a resource subsidy.

Methods

Study sites and sample collection

We surveyed eight boreal lakes in 2017 with a range of DOC from 3.5 to 9.2 mg· L^{-1} at the International Institute for Sustainable Development Experimental Lakes Area (IISD ELA) in northwestern Ontario (49.8283°N, 93.7710°W). The lakes were all small (8.4–56 ha), dimictic, and nutrient poor (5–9 $\mu g \cdot L^{-1}$ total phosphorus), with negligible macrophyte growth (Tonin et al. 2022; Table SA1). The watersheds are dominated by coniferous forest and minimally impacted by development. All the lakes contain populations of White Sucker, which dominate fish biomass in IISD ELA lakes (Chalanchuk 1998), like other boreal lakes across Ontario (Trippel and Harvey 1987). Each lake also has at least one species of piscivore, and variable forage fish communities that include small-bodied percids, leuciscids (North American minnows), coregonids, cottids and gasterosteids (Table SA1). In IISD ELA lakes, there are no observable differences in White Sucker growth rates among lakes with differing piscivore predators (Chalanchuk 1998). Where historical data exist, mean annual DOC concentrations measured in 2017 did not vary by more than 1 $mg \cdot L^{-1}$ from mean annual concentrations determined in the previous 10 years in any lake or by 0.5 $mg \cdot L^{-1}$ for the previous 5 years, with the sole exception of Lake 442, which varied by 1 mg L^{-1}. Previously published data indicate that the abundances and biomass densities of White Sucker in ELA lakes were generally stable in the period leading up to the sampling for this study (Kidd et al. 2014; Rennie et al. 2019), and preliminary assessments suggest that this was true for the other study lakes as well. Epilimnetic water samples were collected either biweekly (four lakes) or monthly (Table SA1) for DOC, particulate and dissolved nutrients (N and P) and chlorophyll *a*, with concurrent profiling for DO, temperature and light using a model LI 192 Underwater Quantum Sensor (Tonin et al. 2022). Water samples were collected using either a 4.5 L integrating sampler (Lakes 223, 224, 239, 373, 442, 626; Shearer 1978) or as a 1 L grab sample collected at 0.5 m depth (Lakes 164, 658) and were analysed in the IISD ELA Chemistry Laboratory using the methods of Stainton et al. (1977) and Havens et al. (2024). Light attenuation (K_d) was calculated from the slope of a regression between the natural logarithm of photosynthetically active radiation (PAR; $\mu mol \cdot m^{-2} \cdot sec^{-1}$) and depth (m) (Fee et al. 1996). We also calculated mean light irradiance, which represents the mean proportion of surface PAR within the water column. Using K_d and mean depth (Z_m), mean light irradiance (I_m) was estimated using the equation of Karlsson et al. (2009):

$$(1) \qquad I_m = \left(1 - e^{K_d \times Z_m}\right) / \left(K_d \times Z_m\right)$$

Fish and invertebrate biomass

We estimated White Sucker relative biomass by deploying 2–3 trap nets (Guzzo et al. 2014) in the littoral zone (<3 m depth) of each lake for 4–6 weeks during the spawning period of spring 2017 (May to mid-June). White Sucker congregate during spawning, so nets were set at known spawning sites. Nets were checked every 2–5 days and White Sucker were enumerated, weighed, and measured for both total and fork length. Mean biomass-per-unit-effort (BPUE) was calculated as the mass of White Sucker (kg) caught per net per day. For any particular lake, all nets were set on the same date within a few hours of each other, left to fish for 2–5 days, and then lifted together on the same day such that they fished for the same number of days. Occasionally, the length of sets varied from one lake to another because of time availability. In our experience, the maximum set time of 5 days is well below the time of net saturation in these study lakes during this time of the year. Fish were collected under permission from the Province of Ontario (License to Collect Fish for Scientific Purposes # 1085769) and the Canadian Council for Animal Care (University of Manitoba Animal Use Protocol #F17-013).

Benthic invertebrate biomass was estimated from collections conducted over a three-week period in August of 2017 using a modified version of the sampling design of Craig et al. (2015). Samples were collected with a gravity corer (7 cm diameter, 38.48 cm^2; Aquatic Research Instruments Gravity NLA corer, Hope, ID, USA) at 4–6 depths in each lake, along five replicate transects. Every lake was sampled at 0.5, 1, 4, and 8 m, except L164, where the deepest sample was collected at 7 m (limited by maximum depth; Table A1). In deeper lakes, samples were also taken at 12 and 18 m, except L626, where the deepest sample was 11.2 m (Table A1). The top 5 cm of each sediment core was retained, sieved through a 500 μm mesh, and preserved in 70% ethanol. Benthic invertebrates were sorted under a dissecting microscope and identified to genus, except Diptera, which were identified to family. Sorting efficiency was evaluated by performing spot checks on 10% of the samples. Less than 10% of the total number of organisms per sample were missed, indicating acceptable sorting efficiency (Environment Canada 2012). Each individual was photographed using a digital microscope camera and body length or shell width measured using ImageJ software (Natural Institutes of Health, U.S.A). Length measurements were converted to mass using published length-weight relationships (Benke et al. 1999; Baumgärtner and Rothhaupt 2003). Benthos biomass was expressed in four ways: as depth-specific means; whole-lake means weighted by the area of each depth zone; littoral means, which were weighted by the area of each sampling depth < 4 m; and profundal means, which were weighted by the area of sampling depths below the thermocline (IISD-Experimental Lakes Area 2023). Functional feeding groups (FFGs) were assigned using Merritt and Cummins (1996).

Zooplankton were collected bi-weekly or monthly by vertically hauling a 50 μm net through the whole water column during the day at the deepest point of the lake ($n = 6$–12 collections per lake) and then counted and converted to biomass following the methods of Tonin et al. (2022).

Samples for stable isotopes

Stable isotopes of H, C, and N were used to determine the direct and indirect utilization of allochthonous (terrestrial) and autochthonous resources by both White Suckers and invertebrates. To estimate allochthonous end members, the stable isotopic composition of terrestrial organic matter was estimated from leaf samples ($n = 27$) collected from trees (*Pinus banksiana*, *Picea mariana*, and *Betula papyrifera*) commonly found near each of the eight lakes. The stable isotope signatures did not statistically differ among watersheds (one-way ANOVA; $F_{7,16}$; $p > 0.5$ for all 3 isotopes), so results were pooled to represent a single terrestrial end member.

To estimate autochthonous phytoplankton end members, water and particulate organic matter (POM) were collected monthly from the epilimnion of each lake. Water samples collected for δ^2H were passed through a 0.2 μm filter and stored at 4 °C in 40 mL glass serum bottles with no headspace. POM was collected by filtering 1–2 L of water with a pre-combusted QM-A filter (nominal pore size = 0.7 μm) and frozen. Stable isotopes in benthic primary producers were determined from periphyton growing on unglazed ceramic tiles that were suspended at 1 m along the shore of each lake. Tiles were initially set out in May and each month thereafter two tiles were removed from each lake, after which periphyton was scraped off, pooled, and frozen ($n = 5$ replicates per lake). Macrophytes were excluded as potential autochthonous end members because macrophyte growth is negligible in our study systems.

To obtain invertebrates for isotopic analysis, littoral benthic invertebrates (benthos) were sampled 2–4 times per lake through June-August at ~1 m depth with a D-framed net and separated by order. Profundal invertebrates were collected using an Ekman grab on 2–4 occasions below the thermocline. Zooplankton were collected monthly ($n = 6$ per lake) by vertically hauling a 150 μm net through the whole water column at the deepest point in the lake. All invertebrates were picked and frozen within 2–4 h of collection. Animals were not depurated before picking.

A single pelvic fin ray was taken from collected White Sucker for stable isotope analysis. To account for potential intra-fin variability, only the tip of each fin ray was used for isotope analysis (Hayden et al. 2015). All fish samples for stable isotope analyses were collected between September to early October to account for the assimilated diet during the open water season based on published tissue turnover rates (Vander Zanden et al. 2015). All White Sucker analyzed were >150 mm in length and assumed to be adults with respect to their feeding ontogeny (Hamilton Stewart 1926). All organic samples were freeze dried or oven-dried at 60°C, homogenized if necessary, and stored in a desiccator until analysis.

The University of Waterloo Environmental Isotope Laboratory analysed δ^{13}C and δ^{15} N using a Finnegan Delta$^{\text{plus}}$ XL-EA mass spectrometer and the Colorado Plateau Stable Isotope Laboratory, Northern Arizona University determined δ^2H following the methods of Doucett et al. (2007) for organic samples, using a correction for exchangeable H using bench-top equilibrium. Water δ^2H was determined using cavity-ring-down laser spectroscopy.

Indirect methods were used to estimate the stable isotopic composition of phytoplankton because they are difficult to isolate from bulk POM. Phytoplankton δ^2H was estimated from δ^2H in water using a photosynthetic fractionation factor of -160.9 ± 17 (Wilkinson et al. 2015). As detailed in Tonin et al. (2022), phytoplankton δ^{13}C and δ^{15} N values were estimated using a C:N ratio mixing model, stable isotopes in bulk POM, and the models of Francis et al. (2011) and Yang et al. (2014). The model of Post et al. (2007) was used to lipid correct zooplankton δ^{13}C values.

Bayesian mixing model

A Bayesian Mixing model, MixSIAR (Stock et al. 2018; R package "Bayesian Mixing models in R", R v4.04), was used to estimate the proportional use of carbon derived from pelagic primary production, littoral benthic primary production, and terrestrial organic matter (allochthony) by both White Sucker and benthic invertebrates. This model uses three matrices: (1) the consumer matrix (isotopic values of White Sucker or benthic invertebrate replicates); (2) the source matrix (lake specific means ± one standard deviation [SD]) of benthic (periphyton) and pelagic (phytoplankton) primary producers, and the mean of allochthonous terrestrial organic matter among all watersheds (±SD); and (3) a matrix of mean (±SD) discrimination factors of the per trophic level enrichment of isotopes.

A trophic discrimination factor for δ^{13}C of 0.4 ± 1.3‰ was used for White Sucker (Post 2002), and 0.0 ± 1‰ for invertebrates (Vander Zanden and Rasmussen 2001). An enrichment factor for δ^{15}N of 2.98 ± 0.97‰ was used for both fish and invertebrates based on the mean of published trophic discrimination factors (Vanderklift and Ponsard 2003). The enrichment of δ^2H across trophic levels by dietary water was corrected for using the model of Solomon et al. (2009):

$$(2) \qquad \omega_{\text{tot}} = 1 - (1 - \omega)^t$$

where ω_{tot} is the proportion of H from dietary water in consumer tissue, t is the trophic position of a consumer above primary producers, and ω is the per-trophic-level contribution of dietary water. A conservative ω value of 0.2 (Wilkinson et al. 2015) was used for fish and zooplankton (following a sensitivity analysis described in Tonin et al. 2022) and a ω value of 0.39 was used for profundal chironomids, which was the mean of values cited for this group in the review of Brett

Table 1. Summary of benthic invertebrate, chironomid, and White Sucker relative biomass estimates among lakes.

	Benthic invertebrate biomass (g·m^{-2})			Chironomid biomass (g·m^{-2})			White Sucker BPUE
Lake	Littoral	Profundal	Whole-lake	Littoral	Profundal	Whole-lake	(kg·net^{-1}·day^{-1} ± SD)
L224	0.17	0.34	0.28	0.08	0.34	0.27	1.27 ± 1.54
L373	0.26	0.06	0.16	0.13	0.06	0.08	1.84 ± 1.44
L223	0.25	0.50	0.42	0.10	0.46	0.32	1.54 ± 0.86
L626	0.54	0.53	0.53	0.07	0.53	0.37	12.84 ± 13.25
L442	0.31	0.14	0.20	0.03	0.14	0.05	0.23 ± 0.09
L239	1.05	0.88	0.94	0.06	0.09	0.08	0.13 ± 0.21
L658	1.14	0.14	0.44	0.09	0.14	0.11	0.24 ± 0.29
L164	0.54	0.49	0.50	0.10	0.49	0.30	1.00 ± 2.07

Note: Littoral means were weighted by area of each sampling depth <4 m, and profundal was weighted by the areas of sampling depths below the thermocline.

et al. (2018). Trophic position (*t*) was estimated from the discrimination factor for δ^{15}N, the mean δ^{15}N of consumers, and δ^{15}N in periphyton (base of the food web) using the formula of Post (2002). Using the proportion of a consumer's dietary water (ω_{tot}) and trophic position, a correction factor for dietary water enrichment was derived as outlined by Berggren et al. (2014):

$$(3)\quad \delta^2H\text{enrichment} = \delta^2H_{\text{sample}} - \left(\delta^2H_{\text{sample}} - \omega_{\text{tot}} \times \delta^2H_{\text{water}}\right) / \left(1 - \omega_{\text{tot}}\right)$$

where δ^2H_{water} is the δ^2H of water, and $\delta^2H_{\text{sample}}$ is the sample being corrected for.

For each model, three Markov chains were run with uninformed Dirichlet priors for 1,000,000 iterations, with a 500,000 iteration burn-in, at a thinning rate of 500 (Stock et al. 2018). The Gelman–Rubin test was used to assess convergence, where models were considered acceptable with a scale reduction factor < 1.1. Medians were used as point estimates because posterior distributions were skewed for some mixing models. Isotopic values were similar among littoral benthic invertebrate orders, so we fitted a single model using a mean value for all littoral invertebrate samples within each lake. Additional mixing models were run to estimate the extent to which White Sucker relied on littoral benthic invertebrates, profundal chironomids and zooplankton where basal primary producers were replaced as "sources" with the isotopic values (±SD) of the potential prey items, adjusted for trophic discrimination. Data used for the isotopic mixing models are summarized in Table SA2 and Fig. SA1 and Fig. SA2.

Statistical analysis

Pearson correlations were used to evaluate hypothesized drivers of White Sucker BPUE and invertebrate biomass, including resource availability, resource utilization, and habitat availability. To further evaluate the relationship between the proportion of lake area with sediments above the photic depth with DOC concentrations and lake morphometry, a multiple regression was also conducted. Model assumptions were assessed visually by comparing quantile-quantile plots and histograms of residuals. White Sucker BPUE was $\log_{10}$ transformed to meet model assumptions.

Probabilities were not corrected for multiple comparisons. Following Muff et al. (2022), we focus here on patterns of statistical significance and the strength of overall evidence rather than emphasizing the results of any single test. Throughout, we give the greatest weight to statistical relationships with probabilities less than 0.01, which provide the strongest evidence of pattern.

Results

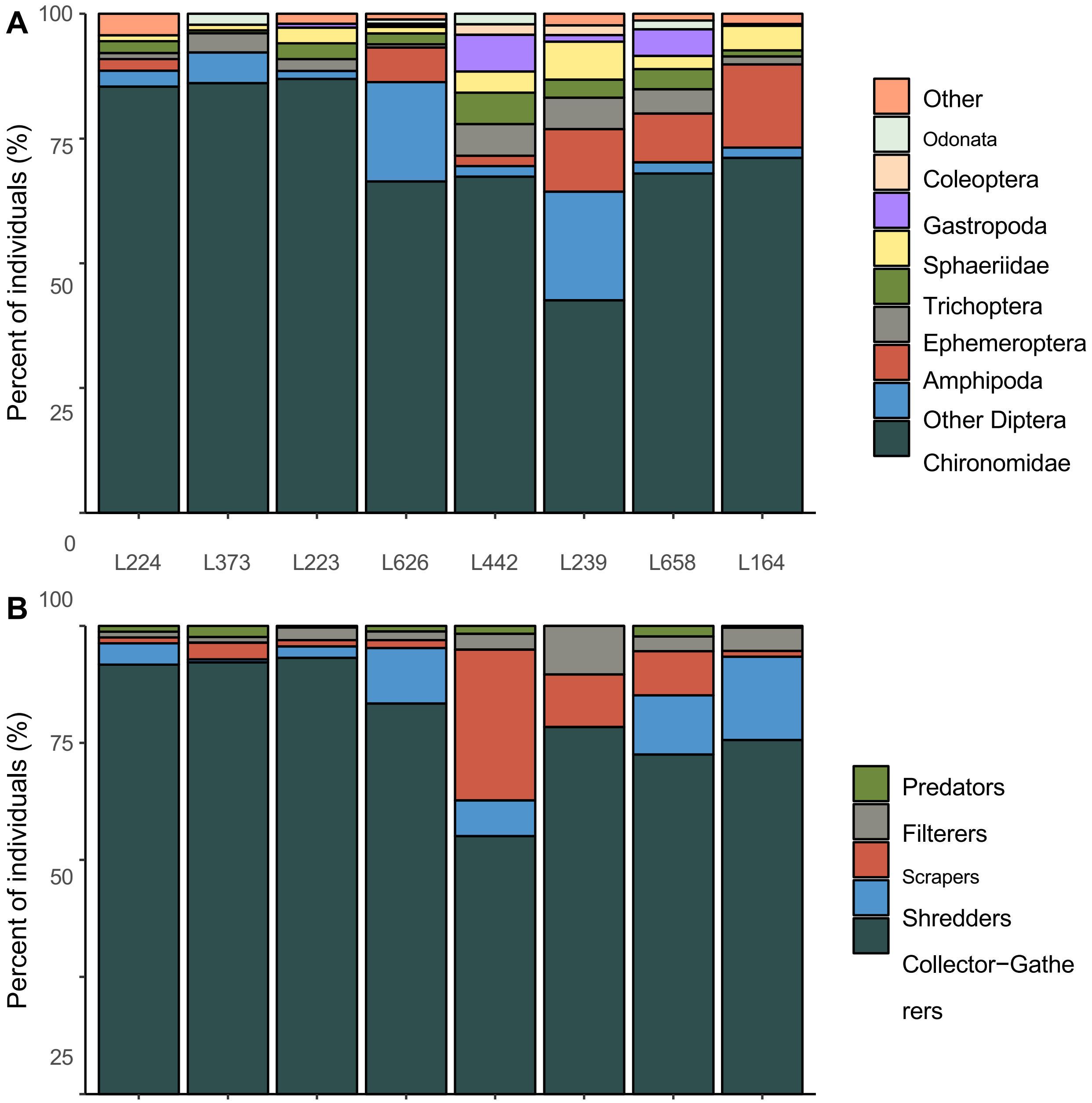
Lake characteristics

Variations in mean DOC concentrations among lakes were correlated with the mean of several limnological characteristics during the ice-free-season (Table SA3; Tonin et al. 2022). Light attenuation ranged from 0.35 to 1.02 m^{-1} and was highly positively correlated with DOC concentrations ($n = 8$, $r = 0.99$, $p < 0.001$), as well as epilimnetic total phosphorus ($n = 8$, $r = 0.91$, $p = 0.002$), and epilimnetic chlorophyll *a* ($n = 8$, $r = 0.93$, $p < 0.0001$), which were positively correlated with each other (Table SA3). Mean light irradiance, which accounts for both light attenuation and lake morphometry (mean depth), was positively correlated with the proportion of lake area above the photic depth (depth of 1% surface PAR; $n = 8$, $r = 0.91$, $p = 0.002$). Similarly, a multiple regression model showed how mean lake depth and DOC concentration influenced the proportion of lake area with sediments above the photic depth (% area above photic depth = 164.9–10.1(DOC [mg· L^{-1}])–6.1(mean depth [m]); $R^2 = 0.76$, $F_{2,5} = 7.68$, $p = 0.03$), where DOC concentration and mean depth account for 46% and 30% of model variance, respectively. DOC concentrations were not significantly correlated with mean or maximum depth, lake area or volume, or volume-weighted hypolimnetic DO (Table SA3; $n = 8$, all $p > 0.05$).

Invertebrate and white sucker biomass

The mean whole-lake depth-weighted biomass of benthic invertebrates ranged from 0.16 to 0.94 g·m^{-2} (Table 1), and mean densities ranged from 1498 to 4215 individuals·m^{-2} among lakes (Table SA4). Chironomids were the dominant taxa in all lakes, accounting for 43% to 87% of individuals in shallow sites (Fig. 1A), and nearly 100% of individuals at deep sites, except for L239, where high densities of amphipods

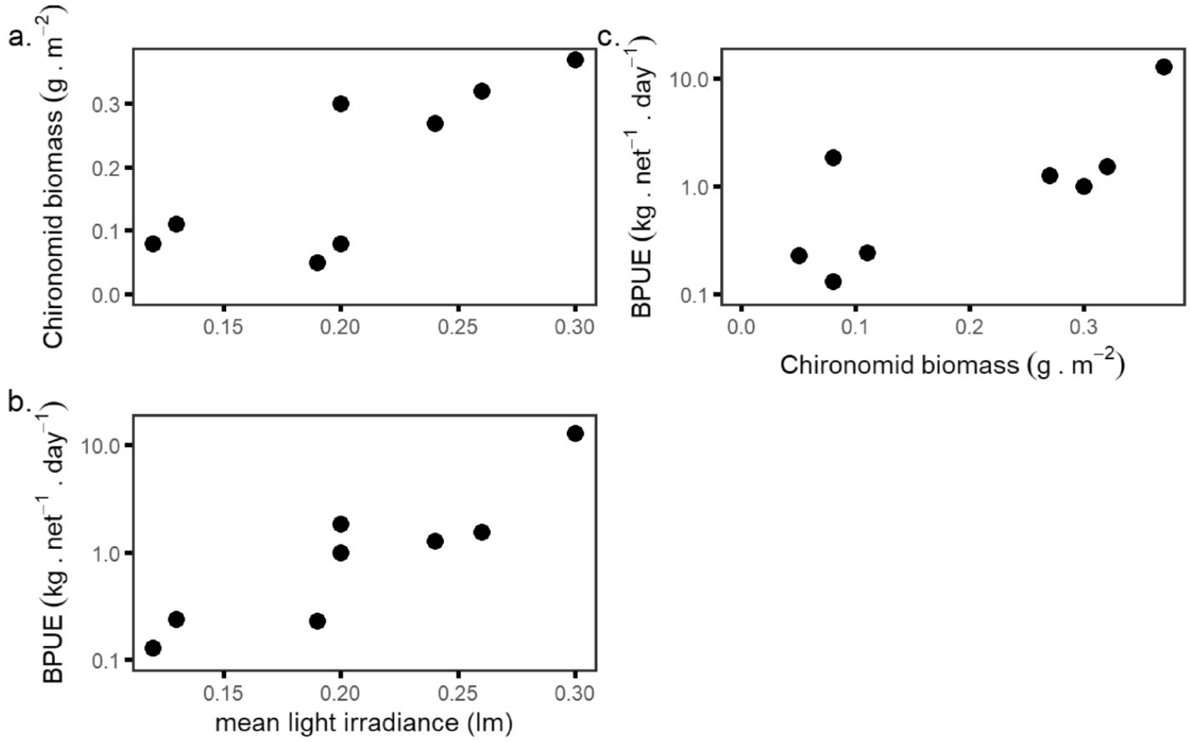
Fig. 1. The relative abundance of benthic invertebrate (A) taxa and (B) functional feeding groups (FFG) in core samples collected at shallow sites (<4 m) among lakes (arranged left to right by increasing DOC concentration).



were encountered at 18 m. At littoral sites, functional feeding groups were dominated by collector-gatherers (Fig. 1B), and the proportion of shredders increased with DOC concentration ($n = 8$, $r = 0.82$, $p = 0.01$), from 1% to 18% of individuals. Mean among-lake benthic biomass was not significantly related to DOC concentration, light attenuation, mean light climate, maximum or mean depth, area, chlorophyll *a*, or TP (Table SA5; $n = 8$; $p > 0.05$). Depth-specific biomass estimates were also not correlated with DO or temperature measured on the day of collection or means for the open water season (Fig. SA3; $n = 42$; $p > 0.05$). Benthic invertebrate biomass was variable at high DO concentrations but was always low at concentrations <2 mg·L^{-1}. Despite this, we found no statistically significant relationships between profundal invertebrate biomass and mean volume-weighted hypolimnetic DO concentration ($n = 8$; $r = 0.01$; $p = 0.98$).

Mean whole-lake chironomid biomass ranged from 0.08 to 0.37 g·m^{-2} and was positively correlated with mean light irradiance (Table SA5; Fig. 2*a*; $n = 8$, $r = 0.84$, $p = 0.01$) and the proportion of lake area above the photic depth ($n = 8$, $r = 0.78$, $p = 0.02$). The biomass of chironomids was similar among lakes in the littoral zone (Table SA4) and the greatest differences in chironomid biomass occurred below the thermocline (profundal zone). Zooplankton biomass ranged from 0.13 to 0.54 g·m^{-2} and was significantly negatively related to DOC concentration ($n = 8$, $r = –0.92$, $p = 0.001$; Tonin et al. 2022).

Fig. 2. (*a*) Mean whole-lake chironomid biomass in relation to mean light irradiance ($n = 8$; $r = 0.82$, $p = 0.01$), and (*b*) $_{\log 10}$ White Sucker biomass catch-per-unit-effort (BPUE) in relation to mean light irradiance ($r = 0.90$; $p = 0.002$), and (*c*) mean whole-lake chironomid biomass ($r = 0.74$, $p = 0.04$). Note log scale of *y*-axis on panels b and c.



White Sucker BPUE ranged from 0.13 to 12.8 kg·net^{-1}·day^{-1}. Although White Sucker BPUE was not significantly correlated with DOC concentrations (Table SA5; $n = 8$, $r = -0.56$, $p = 0.15$), it was positively related to mean light irradiance (Fig. 2*b*; $n = 8$, $r = 0.90$, $p = 0.002$), the proportion of lake area above the photic depth ($n = 8$, $r = 0.89$, $p = 0.004$) and mean whole-lake chironomid biomass (Fig. 2*c*; $n = 8$, $r = 0.75$, $p = 0.03$). Total phosphorus, epilimnetic chlorophyll *a*, mean depth, and mean benthic invertebrate biomass or zooplankton biomass were not significantly correlated with White Sucker BPUE ($n = 8$, $p > 0.05$).

Resource use

Terrestrial organic matter (t-OM) δ^2H values were higher than periphyton by 22‰ (±3.6‰) and phytoplankton by 46‰ (±4.3‰), on average (±SD) (Fig. SA1). There was also strong isotopic separation among end members using δ^{15}N signatures, with t-OM being most depleted on average (–5.5‰ ± 1.6‰ versus 1.1‰ ± 1.3 δ^{15}N for periphyton, and 1.9‰ ± 1.5 δ^{15}N for phytoplankton). Terrestrial organic matter and epilimnetic phytoplankton had similar δ^{13}C values on average, but both were more negative than periphyton by 4–8‰ within each lake.

Median littoral benthic invertebrate allochthony ranged from 27% to 45% (median of posterior estimate) among lakes (Table SA6) and was positively correlated with DOC concentration (Fig. 3*a*; $n = 8$, $r = 0.83$, $p = 0.01$) and light attenuation ($n = 8$, $r = 0.80$, $p = 0.02$). In most lakes, profundal chironomids were more depleted in δ^{13}C than epilimnetic phytoplankton and terrestrial organic matter (Table SA2), as well as metalimnetic POM (Tonin et al. 2022). As a result, profundal chironomid stable isotope ratios fell outside of the mixing polygons based on terrestrial organic matter, phytoplankton, and periphyton and meaningful model results could not be generated. This implies that an important resource used by profundal chironomids was missed in our sampling. Profundal chironomid δ^{13}C values ranged from –30.4‰ to –41.9‰ (Table SA2), suggesting possible contributions from methanotrophic bacteria (Supplement B).

White Sucker allochthony ranged from 26% to 48% (medians of posterior distribution; Table SA7) and like littoral benthic invertebrates, was positively related with DOC concentration (Fig. 3*b*; $n = 8$, $r = 0.86$, $p = 0.007$) and light attenuation ($n = 8$, $r = 0.88$, $p = 0.004$), but also negatively correlated with mean light irradiance ($n = 8$, $r = –0.79$, $p = 0.02$). Correspondingly, White Sucker allochthony was also positively related to littoral benthic invertebrate allochthony (Fig. SA4; $r = 0.83$, $p = 0.01$). Utilization of littoral primary producers by White Suckers ranged from 9% to 55% but was not related to DOC concentration or light attenuation (Table SA7; $n = 8$; $p > 0.1$). The main dietary items supporting White Suckers as indicated from mixing models were benthic invertebrates (profundal + littoral), which accounted for 56% to 88% of White Sucker diet (Table SA8). Although chironomid biomass was a strong predictor of White Sucker BPUE, we found no relationship between BPUE and reliance on benthic invertebrates ($n = 8$, $r = 0.52$, $p = 0.19$; profundal + littoral) or between BPUE and reliance on profundal

Fig. 3. Patterns of allochthony for (*a*) littoral benthic invertebrates and (*b*) White Sucker in relation to DOC concentration. Boxplots represent the 5th, 25th, 50th, 75th, and 95th percentiles of the posterior distribution from MixSIAR models.

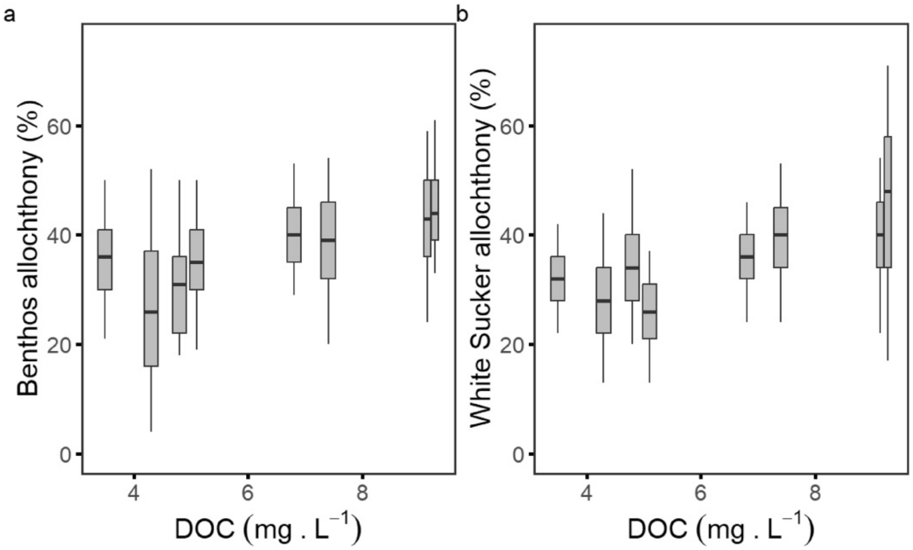
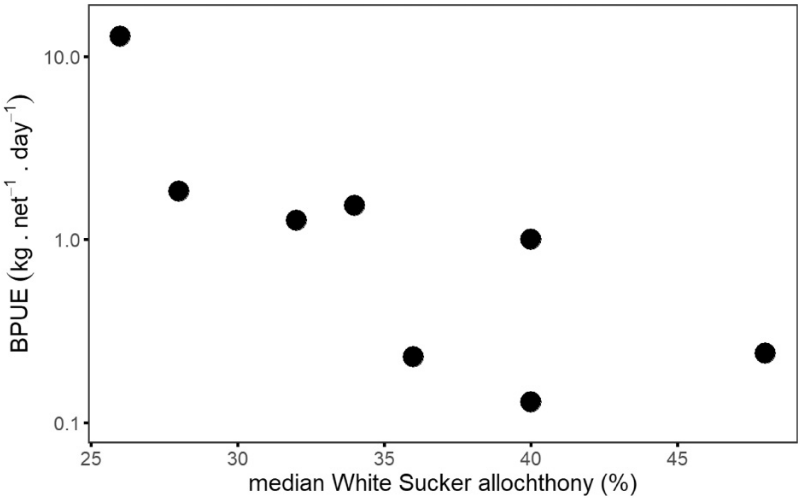


Fig. 4. The relationship between White Sucker biomass-catch-per-unit-effort (BPUE) and allochthony ($r = -0.82$, $p = 0.01$). Allochthony estimates are presented as medians from the posterior distribution of the Bayesian mixing model. Note: the *y*-axis is $_{\log10}$ transformed.



chironomids ($n = 8$, $r = 0.56$, $p = 0.15$). White Sucker reliance on benthic invertebrates, which include chironomids, was also not related to mean whole-lake chironomid biomass (Fig. SA5; $n = 8$, $r = 0.33$, $p = 0.42$). However, BPUE was negatively correlated with White Sucker allochthony (Fig. 4; $n = 8$, $r = -0.82$, $p = 0.01$). Based on mixing model results, zooplankton accounted for 12% to 44% of White Sucker diet, but the proportion of zooplankton in White Sucker diet was not significantly correlated with DOC concentration ($n = 8$, $r = 0.60$, $p = 0.12$).

Discussion

Our results highlight how mean light irradiance, which is a function of both DOC concentration and lake depth, may affect variation in White Sucker relative biomass in eight nutrient-poor, boreal lakes by influencing the availability of benthic invertebrate resources. Our results support other among-lake surveys that have demonstrated negative relationships between fish biomass and light attenuation and DOC concentrations (Karlsson et al. 2009; Finstad et al. 2014; Karlsson et al. 2015; Benoit et al. 2016; Horppila et al. 2025). The relative biomass of White Sucker was not significantly correlated with DOC concentrations alone likely because the effect of DOC on mean light irradiance is moderated by lake depth and basin morphometry. Deeper lakes are comparatively more vulnerable to increased DOC loading because a greater proportion of lake area falls below the photic depth, relative to shallower lakes of the same DOC concentration (Finstad et al. 2014). In our study, White Sucker relative biomass was lowest in lakes with a high proportion of their volume outside of the photic zone.

Our study identifies two potential mechanisms behind our observed negative relationship between mean light irradiance and fish relative biomass. First, White Sucker and benthic invertebrate usage of t-OM, increased in low light (high DOC) lakes. Although t-OM contributed a considerable proportion of the overall resource use of benthic invertebrates, it is generally considered to be a poor-quality resource compared to autochthonous production (Brett et al. 2017), potentially affecting benthic invertebrate productivity. Based on mixing models, benthic invertebrates were the primary prey of White Sucker, suggesting indirect utilization of terrestrial carbon through invertebrate consumption. Although White Sucker may also consume terrestrial organic matter directly, this is only observed when invertebrate prey are scarce (Ahlgren 1990). Second, chironomid biomass was positively correlated with mean light irradiance, suggesting that resource limitation of benthivorous fish may be greater in low light (high DOC) lakes. Similar to the findings of Karlsson et al. (2015), we observed declines in White Sucker BPUE with increasing allochthony, suggesting that terrestrial organic matter is not a sufficient resource subsidy to offset the effects of decreased light penetration on primary production.

Methane-oxidizing bacteria (MOB) were not included as a potential energy pathway in our mixing models, which could artificially bias our allochthony estimates towards relatively higher phytoplankton use. To examine this possibility, we explored the potential contribution of MOB using a series of hypothetical models (Supplement B). These models indicate that the potential contribution of methane oxidizing bacteria to White Sucker biomass via profundal chironomids was likely less than 11% (Table SB3), suggesting that any bias due to methanotrophs is probably minimal. Instead, the comparatively high usage of phytoplankton-based carbon by White Suckers in our lakes as compared to other studies (e.g., Karlsson et al. 2009) may be related to greater predation upon profundal chironomids (between 10% to 57% of White Sucker diets; Table SA7) that likely rely more on pelagic energy pathways.

Across our study lakes, the decline in White Sucker BPUE with decreasing light availability occurred with concomitant decreases in chironomid densities, which are favoured prey of White Suckers (Hamilton Stewart 1926; Trippel and Harvey 1987). Lakes with higher DOC concentrations often have lower benthic invertebrate biomass because DOC-mediated light limitation may suppress benthic primary production (Karlsson et al. 2009; Godwin et al. 2014; Norman et al. 2022). White Sucker are strongly linked to the benthic food web and other studies also suggest that variation in benthic invertebrate biomass and chironomid density can affect White Sucker biomass and growth (Trippel and Harvey 1987). In our study lakes, resource limitation may have been further exacerbated by decreases in pelagic primary production and zooplankton due to the influence of DOC on light penetration in these lakes (Tonin et al. 2022; Sherbo et al. 2023).

While DOC affects stratification and the vertical distribution of oxygen and temperature, potentially affecting the availability of suitable oxythermal habitat (Craig et al. 2015), this does not appear to be the case in our study. In our lakes, depth-specific benthic biomass was not correlated with temperature or dissolved oxygen concentration (Fig. SA3). In general, benthic invertebrate biomass decreased with increasing depth within our study lakes, and biomass was consistently low at DO concentrations below 2 mg $O_2 \cdot L^{-1}$. Chironomid biomass was variable at higher DO concentrations (Fig. SA3a), suggesting that DO concentration may influence invertebrate biomass, but other factors are also important. Chironomid biomass in our study lakes tended to be greater at deep sites relative to shallow sites, and we found no statistical relationship between profundal chironomid biomass and volume-weighted hypolimnetic oxygen. Because chironomids can tolerate periods of anoxia and may have lower oxygen thresholds than many fish species, it is possible that low dissolved oxygen concentrations may provide a refuge to chironomids from predation (Jónasson 1984). Lower chironomid densities at shallower sites may also reflect higher inshore predation by minnows and other taxa.

At littoral sites, utilization of benthic primary production by invertebrates declined with increasing DOC concentrations, but littoral benthic invertebrate biomass was not related to utilization of this resource or DOC concentration. The lack of a relationship between these two variables may reflect changes in benthic invertebrate community composition with increasing DOC concentration. Benthic invertebrates are a diverse group with various feeding strategies; the loss of benthic primary production with increasing DOC concentrations may drive changes in community composition that favour detrital, or other feeding strategies while maintaining total invertebrate biomass. In support of this observation, the proportion of benthic invertebrates at littoral sites belonging to the functional feeding group “shredders” increased with DOC concentration in our lakes, from 1–18% of individuals.

Given changes in light penetration with increasing DOC concentrations observed here and elsewhere, declines in fish and benthic invertebrate biomass may be related to decreases in whole-lake primary production (both benthic and pelagic). Whole-lake energy mobilization per m^2 or m^3 typically declines with increasing light attenuation and increasing lake depth, because a greater proportion of lake area and volume falls below the photic depth in deep lakes relative to shallow lakes with similar light attenuation (Ask et al. 2009; Finstad et al. 2014). In our lakes, whole-lake mean chironomid biomass and White Sucker BPUE were both positively correlated with the proportion of lake area with light $>1\%$ surface PAR (compensation depth), which was related to both DOC and mean depth.

Though our findings are based on a limited number of small, dimictic boreal lakes and focus on a single species of fish, White Sucker, they are broadly consistent with the results of studies of other fish species, including Perch and Roach (Karlsson et al. 2015; Seekell et al. 2018; Horppila et al. 2025), Bluegill (Craig et al. 2017), Walleye, and Trout (Finstad et al. 2014; Benoit et al. 2016). Lakes of different sizes, mixing patterns, and fish species may respond differently to inputs of terrestrial organic matter. White Sucker are a species that is tightly linked to benthic food webs and other fish species that are more flexible in their feeding ecology may not respond in a similar manner to declines in benthic prey. For example, Johnston et al. (2019) found that the δ^{13}C signatures of White Sucker became more littoral (less negative) in clearer lakes whereas the δ^{13}C signatures of Lake Trout were unaffected. However, the consistency of our results with other species that feed more broadly suggests that DOC impacts on energy transfer to fish are broader than just the feeding mode of the species under study.

While our benthic invertebrate biomass estimates were determined from a single annual survey and do not account for temporal variations, other work in the boreal ecozone region has shown that benthic invertebrate densities are relatively stable seasonally (Shchapov and Ozersky 2024). Further, our main method of quantitative benthic sampling (i.e., sediment coring) arguably did not efficiently collect larger mobile invertebrate taxa. However, chironomids that are not highly mobile numerically dominate the benthic communities of IISD ELA lakes (Hamilton 1971) and are the primary prey for White Sucker (Hamilton Stewart 1926; Trippel and Harvey 1987). This suggests that the potential bias against large taxa in our benthic surveys likely had little impact on our results.

Our results support a growing body of literature indicating that DOC-mediated light limitation results in reductions in standing biomass in several ecosystem components (Karlsson et al. 2009; Finstad et al. 2014; Seekell et al. 2018; Norman et al. 2022; Horppila et al. 2025), and provides evidence for two, non-mutually exclusive mechanisms that link declines in fish biomass with DOC-mediated light limitation. First, we found support for the conceptual model that changes in mean light irradiance and its effects on primary production influence the availability of benthic invertebrate prey, thereby affecting fish biomass (Karlsson et al. 2009; Craig et al. 2015). Second, White Sucker biomass declined with increasing allochthony (Karlsson et al. 2015), suggesting that terrestrial organic matter is not a resource subsidy relative to losses of benthic and pelagic primary production in high DOC environments. Given the similarity of our results with surveys of other fish populations that utilize a wide variety of different habitats and feeding strategies (Finstad et al. 2014; Karlsson et al. 2015; Benoit et al. 2016; Craig et al. 2017; Seekell et al. 2018; Horppila et al. 2025), our results suggest that increases of DOC concentrations are likely to lead to reductions in fish productivity.

Acknowledgements

We thank the staff of IISD ELA, and particularly Justin Budyk, Lee Hrenchuk, Lauren Hayhurst, Ken Sandilands, and Paul Faford for their field and laboratory support. Additional support in the field from Bryanna Sherbo (University of Manitoba) and Rachel Henderson (University of Waterloo) is also greatly appreciated. Nutrient analyses were completed by the IISD ELA Chemical Laboratory under the direction of Sonya Havens. Funding was provided by a Manitoba Hydro award to SNH, MJP and MDR, support from an NSERC discovery grant, and the Canadian Foundation for Innovation to MDR and MITACS, IISD ELA Graduate Fellowship, and Fish Futures Inc. awards to JT.

Article information

History dates

Received: 28 October 2024
Accepted: 20 February 2025
Accepted manuscript online: 28 February 2025
Version of record online: 24 March 2025

Notes

This paper is part of a Collection entitled Freshwater browning and coastal darkening: effects and processes.

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Data availability

Data are available in Figshare.com: https://doi.org/10.6084/m9.figshare.13125278.v1 and https://doi.org/10.6084/m9.figshare.27316146.v1.

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Competing interests

The authors declare there are no competing interests.

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2024-0338.

References

Ahlgren, M.O. 1990. Diet selection and the contribution of detritus to the diet of the juvenile white sucker (*Catostomus commersoni*). Can. J. Fish. Aquat. Sci. **47**(1): 41–48. doi:10.1139/f90-004.

Ask, J., Karlsson, J., Persson, L., Ask, P., Bystrom, P., and Jansson, M. 2009. Whole-lake estimates of carbon flux through algae and bacteria in benthic and pelagic habitats of clear-water lakes. Ecology, **90**(7): 1923–1932. doi:10.1890/07-1855.1. PMID: 19694140.

Baumgärtner, D., and Rothhaupt, K.-O. 2003. Predictive length–dry mass regressions for freshwater invertebrates in a pre-alpine lake littoral. Int. Rev. Hydrobiol. **88**(5): 453–463. doi:10.1002/iroh.200310632.

Benke, A.C., Huryn, A.D., Smock, L.A., and Wallace, J.B. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. J. N. Am. Benthol. Soc. **18**(3): 308–343. doi:10.2307/1468447.

Benoit, P.O., Beisner, B.E., and Solomon, C.T. 2016. Growth rate and abundance of common fishes is negatively related to dissolved organic carbon concentration in lakes. Can. J. Fish. Aquat.Sci. **73**(8): 1230–1236. doi:10.1139/cjfas-2015-0340.

Berggren, M., Ziegler, S.E., St-Gelais, N.F., Beisner, B.E., and del Giorgio, P.A. 2014. Contrasting patterns of allochthony among three major groups of crustacean zooplankton in boreal and temperate lakes. Ecology, **95**(7): 1947–1959. doi:10.1890/13-0615.1. PMID: 25163126.

Berglund, J., Müren, U., Båmstedt, U., and Andersson, A. 2007. Efficiency of a phytoplankton-based and a bacterial-based food web in a pelagic marine system. Limnol. Oceanogr. **52**(1): 121–131. doi:10.4319/lo.2007.52.1.0121.

Brett, M.T., Holtgrieve, G.W., and Schindler, D.E. 2018. An assessment of assumptions and uncertainty in deuterium-based estimates of terrestrial subsidies to aquatic consumers. Ecology, **99**(5): 1073–1088. doi:10.1002/ecy.2211. PMID: 29714826.

Brett, M.T., Kainz, M.J., Taipale, S.J., and Seshan, H. 2009. Phytoplankton, not allochthonous carbon, sustains herbivorous zooplankton production. Proc. Natl. Acad. Sci. **106**(50): 21197–21201. doi:10.1073/pnas.0904129106.

Brett, M.T., Bunn, S.E., Chandra, S., Galloway, A.W.E., Guo, F., Kainz, M.J., et al. 2017. How important are terrestrial organic carbon inputs for secondary production in freshwater ecosystems? Freshwater Biol. **62**(5): 833–853. doi:10.1111/fwb.12909.

Chalanchuk, S.M. 1998. Growth of white sucker, *catastomus commersoni*, in thirty-one lakes at the Experimental Lakes Area, northwestern Ontario. Canadian Technical Report of Fisheries and Aquatic Sciences 2207, Fisheries and Oceans, Winnipeg. vi + 65p.

Craig, N., Jones, S.E., Weidel, B.C., and Solomon, C.T. 2015. Habitat, not resource availability, limits consumer production in lake ecosystems. Limnol. Oceanogr. **60**(6): 2079–2089. doi:10.1002/lno.10153.

Craig, N., Jones, S.E., Weidel, B.C., and Solomon, C.T. 2017. Life history constraints explain negative relationship between fish productivity and dissolved organic carbon in lakes. Ecol. Evol. **7**(16): 6201–6209. doi:10.1002/ece3.3108. PMID: 28861225.

Creed, I.F., Bergström, A.-K., Trick, C.G., Grimm, N.B., Hessen, D.O., Karlsson, J., et al. 2018. Global change-driven effects on dissolved organic matter composition: implications for food webs of northern lakes. Global Change Biol. **24**(8): 3692–3714. doi:10.1111/gcb.14129.

de Wit, H. A., Stoddard, J. L., Monteith, D. T., Sample, J. E., Austnes, K., Couture, S., et al. 2021. Cleaner air reveals growing influence of climate on dissolved organic carbon trends in northern headwaters. Environ. Res. Lett. **16**: 104009. doi:10.1088/1748-9326/ac2526.

Doucett, R., Marks, J.C., Blinn, D.W., Caron, M., and Hungate, B.A. 2007. Measuring terrestrial subsidies to aquatic food webs using stable isotopes of hydrogen. Ecology, **88**(6): 1587–1592. doi:10.1890/06-1184. PMID: 17601150.

Environment Canada. 2012. Metal mining technical guidance for environmental effects monitoring. 549pp. doi:En14-61/2012E-PDF.

Fee, E.J., Hecky, R.R., Kasian, S.E.M., and Cruikshank, D.R. 1996. Effects of lake size, water clarity, and climatic variability on mixing depths in Canadian Shield lakes. Limnol. Oceanogr. **41**(5): 912–920. doi:10.4319/lo.1996.41.5.0912.

Finstad, A.G., Helland, I.P., Ugedal, O., Hesthagen, T., and Hessen, D.O. 2014. Unimodal response of fish yield to dissolved organic carbon. Ecol. Lett. **17**(1): 36–43. doi:10.1111/ele.12201. PMID: 24165396.

Francis, T.B., Schindler, D.E., Holtgrieve, G.W., Larson, E.R., Scheuerell, M.D., Semmens, B.X., and Ward, E.J. 2011. Habitat structure determines resource use by zooplankton in temperate lakes. Ecol. Lett. **14**(4): 364–372. doi:10.1111/j.1461-0248.2011.01597.x. PMID: 21314881.

Godwin, S.C., Jones, S.E., Weidel, B.C., and Solomon, C.T. 2014. Dissolved organic carbon concentration controls benthic primary production: results from in situ chambers in north-temperate lakes. Limnol. Oceanogr. **59**(6): 2112–2120. doi:10.4319/lo.2014.59.6.2112.

Guzzo, M.M., Rennie, M.D., and Blanchfield, P.J. 2014. Evaluating the relationship between mean catch per unit effort and abundance for littoral cyprinids in small boreal shield lakes. Fish. Res. **150**: 100–108. doi:10.1016/j.fishres.2013.10.019.

Hamilton, A.L. 1971. Zoobenthos of fifteen lakes in the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Board Can. **28**(2): 257–263. doi:10.1139/f71-036.

Hamilton Stewart, N. 1926. Development, growth, and food habits of the White Sucker, *Catostomus commersonii* Lesueur. Bull. Bur. Fish. **42**: 146–184.

Havens, S.M., Cooney, B.T., and Stainton, M.P. 2024. The chemical analysisof fresh water (3rd ed.). International Institute for Sustainable Development. pp. 274. doi:10.13140/RG.2.2.32178.82889.

Hayden, B., Soto, D.X., Jardine, T.D., Graham, B.S., Cunjak, R.A., Romakkaniemi, A., and Linnansaari, T. 2015. Small tails tell tall tales—intra-individual variation in the stable isotope values of fish fin. PLoS One, **10**(12): e0145154. doi:10.1371/journal.pone.0145154. PMID: 26670464.

Horppila, J., Nurminen, L., Rajala, S., and Estlander, S. 2025. The effect of water colour on fish communities in boreal lakes. Ecosystems, **28**: 3. doi:10.1007/s10021-024-00954-5.

IISD-Experimental Lakes Area. 2023. IISD Experimental Lakes Area: Bathymetry data package. 1968-2023 ver 4. Available from https://portal.edirepository.org/nis/mapbrowse?packageid=edi.1276.3.

Jane, S.F., Detmer, T.M., Larrick, S.L., Rose, K.C., Randall, E.A., Jirka, K.J., and McIntyre, P.B. 2024. Concurrent warming and browning eliminate cold-water fish habitat in many temperate lakes. Proc. Natl. Acad. Sci. **121**(2): e2306906120. doi:10.1073/pnas.2306906120.

Johnston, T.A., Ehrman, A.D., Hamilton, G.L., Nugent, B.K., Cott, P.A., and Gunn, J.M. 2019. Plenty of room at the bottom: niche variation and segregation in large-bodied benthivores of boreal lakes. Can. J. Fish. Aquat. Sci. **76**(8): 1411–1422. doi:10.1139/cjfas-2018-0180.

Jónasson, P.M. 1984. Oxygen demand and long term changes of profundal zoobenthos. Hydrobiologia, **115**(1): 121–126. doi:10.1007/bf00027905.

Karlsson, J., Bystrom, P., Ask, J., Ask, P., Persson, L., and Jansson, M. 2009. Light limitation of nutrient-poor lake ecosystems. Nature, **460**(7254): 506–509. doi:10.1038/nature08179. PMID: 19626113.

Karlsson, J., Bergstrom, A.-K., Bystrom, P., Gudasz, C., Rodriguez, P., and Hein, C. 2015. Terrestrial organic matter input suppresses biomass production in lake ecosystems. Ecology, **96**(11): 2870–2876. doi:10.1890/15-0515.1. PMID: 27070007.

Kelly, P.T., Solomon, C.T., Weidel, B.C., and Jones, S.E. 2014. Terrestrial carbon is a resource, but not a subsidy, for lake zooplankton. Ecology, **95**(5): 1236–1242. doi:10.1890/13-1586.1. PMID: 25000755.

Kidd, K.A, Paterson, M.J, Rennie, M.D., Podemski, C.L., Findlay, D.L., Blanchfield, P.J., and Liber, K. 2014. Responses of a freshwater food web to a potent synthetic oestrogen. Philos. Trans. R. Soc. B: Biol. Sci. **369**: 20130578. doi:10.1098/rstb.2013.0578.

Merritt, R.W., and Cummins, K.W. 1996. An introduction to the aquatic insects of North America. Kendall/Hunt, Dubuque, Iowa.

Muff, S., Nilsen, E.B., O'Hara, R.B., and Nater, C.R. 2022. Rewriting results sections in the language of evidence. Trends Ecol. Evol. **37**(3): 203–210. doi:10.1016/j.tree.2021.10.009. PMID: 34799145.

Norman, S., Nilsson, K.A., Klaus, M., Seekell, D., Karlsson, J., and Byström, P. 2022. Effects of habitat-specific primary production on fish size, biomass, and production in northern oligotrophic lakes. Ecosystems, **25**: 1555–1570. doi:10.1007/s10021-021-00733-6.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology, **83**(3): 703–718. doi:10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2.

Post, D.M., Layman, C.A., Arrington, D.A., Takimoto, G., Quattrochi, J., and Montaña, C.G. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia, **152**(1): 179–189. doi:10.1007/s00442-006-0630-x. PMID: 17225157.

Rennie, M.D., Kennedy, P.J., Mills, K.H., Rodgers, C.M.C, Charles, C., Hrenchuk, L., et al. 2019. Impacts of an experimental aquaculture operation on fish communities: A whole-ecosystem approach. Freshwater Biol. **64**: 870–885. doi:10.1111/fwb.13269.

Seekell, D.A., Byström, P., and Karlsson, J. 2018. Lake morphometry moderates the relationship between water color and fish biomass in small boreal lakes. Limnol. Oceanogr. **63**(5): 2171–2178. doi:10.1002/lno.10931.

Shearer, J.A. 1978. Two devices for obtaining water samples integrated over depth. Canadian Fisheries and Marine Service Technical Report 772, Winnipeg. iv + 9p

Sherbo, B., Tonin, J., Paterson, M.J., Hann, B.J., Kozak, J., and Higgins, S.N. 2023. The effects of terrestrial dissolved organic matter on phytoplankton biomass and productivity in boreal lakes. Freshwater Biol. **68**(12): 2109–2119. doi:10.1111/fwb.14178.

Shchapov, K., and Ozersky, T. 2024. Full year seasonality of benthos in the nearshore of Lake Superior. J. Great Lakes Res. **51**: 102314. doi:10.1016/j.jglr.2024.102314.

Solomon, C., Cole, J., Doucett, R., Pace, M., Preston, N., Smith, L., and Weidel, B. 2009. The influence of environmental water on the hydrogen stable isotope ratio in aquatic consumers. Oecologia, **161**(2): 313–324. doi:10.1007/s00442-009-1370-5. PMID: 19471971.

Solomon, C.T., Carpenter, S.R., Clayton, M.K., Cole, J.J., Coloso, J.J., Pace, M.L., et al. 2011. Terrestrial, benthic, and pelagic resource use in lakes: results from a three-isotope bayesian mixing model. Ecology, **92**(5): 1115–1125. doi:10.1890/10-1185.1. PMID: 21661572.

Solomon, C.T., Jones, S.E., Weidel, B.C., Buffam, I., Fork, M.L., Karlsson, J., et al. 2015. Ecosystem consequences of changing inputs of terrestrial dissolved organic matter to lakes: current knowledge and future challenges. Ecosystems, **18**: 376–389. doi:10.1007/s10021-015-9848-y.

Stainton, M.P., Capel, M.J., and Armstrong, F.A.J. 1977. The chemical analysis of fresh water. Fish. Res. Board Can. Misc. Spec. Publ. **25**: 125p.

Stasko, A. D., Gunn, J.M., and Johnston, T.A. 2012. Role of ambient light in structuring north-temperate fish communities: potential effects of increasing dissolved organic carbon concentration with a changing climate. Environ. Rev. **20**(3): 173–190. doi:10.1139/a2012-010.

Stock, B.C., Jackson, A.L., Ward, E.J., Parnell, A.C., Phillips, D.L., and Semmens, B.X. 2018. Analyzing mixing systems using a new generation of Bayesian tracer mixing models. PeerJ, **6**: e5096. doi:10.7717/peerj.5096.

Tonin, J., Sherbo, B., Higgins, S.N., Schiff, S.L., and Paterson, M.J. 2022. Dissolved organic carbon affects the occurrence of deep chlorophyll peaks and zooplankton resource use and biomass. Freshwater Biol. **67**(8): 1357–1369. doi:10.1111/fwb.13922.

Trippel, E.A., and Harvey, H.H. 1987. Abundance, growth, and food supply of white suckers (*Catostomus commersoni*) in relation to lake morphometry and pH. Can. J. Zool. **65**(3): 558–564. doi:10.1139/z87-086.

Vander Zanden, M.J., and Rasmussen, J.B. 2001. Variation in δ15N and δ13C trophic fractionation: implications for aquatic food web studies. Limnol. Oceanogr. **46**(8): 2061–2066. doi:10.4319/lo.2001.46.8.2061.

Vander Zanden, M.J., Clayton, M.K., Moody, E.K., Solomon, C.T., and Weidel, B.C. 2015. Stable isotope turnover and half-life in animal tissues: a literature synthesis. PLoS One, **10**(1): e0116182. doi:10.1371/journal.pone.0116182. PMID: 25635686.

Vanderklift, M.A., and Ponsard, S. 2003. Sources of variation in consumer-diet δ 15 N enrichment: a meta-analysis. Oecologia, **136**(2): 169–182. doi:10.1007/s00442-003-1270-z. PMID: 12802678.

Wilkinson, G.M., Pace, M.L., and Cole, J.J. 2013. Terrestrial dominance of organic matter in north temperate lakes. Global Biogeochem. Cycles, **27**(1): 43–51. doi:10.1029/2012GB004453.

Wilkinson, G.M., Cole, J.J., and Pace, M.L. 2015. Deuterium as a food source tracer: sensitivity to environmental water, lipid content, and hydrogen exchange. Limnol. Oceanogr.: Methods, **13**(5): 213–223. doi:10.1002/lom3.10019.

Yang, C., Wilkinson, G.M., Cole, J.J., Macko, S.A., and Pace, M.L. 2014. Assigning hydrogen, carbon, and nitrogen isotope values for phytoplankton and terrestrial detritus in aquatic food web studies. Inland Waters, **4**(2): 233–242. doi:10.5268/IW-4.2.700.