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Growth rate and abundance of common fishes is negatively related to dissolved organic carbon concentration in lakes

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Abstract

Dissolved organic carbon (DOC) can limit food web productivity in lakes, potentially imposing resource limitation on fishes. We asked whether the abundance or early growth rate of three fish species was negatively related to DOC in 59 lakes in southern Québec, Canada, where DOC concentrations ranged from 4 to 16 mg L⁻¹ for lakes containing walleye (*Sander vitreum*) and yellow perch (*Perca flavescens*) and from 2.6 to 9 mg L⁻¹ for lakes containing lake trout (*Salvelinus namaycush*). Estimates of abundance and growth rate were more precise for walleye and lake trout than for yellow perch due to differences in sample size. Abundance was negatively related to DOC for walleye, and perhaps also for lake trout and yellow perch. Early growth rate was negatively related to DOC for walleye and lake trout, but not yellow perch. These results support a growing body of literature suggesting that the productivity of fish populations may be negatively related to DOC concentrations in lakes.

Keywords: dissolved organic carbon, allochthonous organic matter, fish, food web, productivity

Résumé

Le carbone organique dissous (COD) peut limiter la productivité à l'intérieur des réseaux trophiques dans les lacs, imposant une limitation potentielle des ressources disponibles pour les poissons. Nous avons testé si l'abondance ou le taux de croissance juvénile de trois espèces de poissons étaient négativement liés à la concentration en COD dans 59 lacs du sud de la province du Québec, Canada, où la concentration en COD variait entre 4 et 16 mg L⁻¹ pour les lacs incluant le doré jaune (*Sander vitreum*) et la perchaude (*Perca flavescens*) et entre 2,6 et 9 mg L⁻¹ pour ceux incluant le touladi (*Salvelinus namaycush*). Les estimations d'abondance et les taux de croissance étaient plus précis pour le doré jaune et pour le touladi par rapport à la perchaude,

33 due à une différence au niveau de la taille d'échantillon. L'abondance était négativement reliée
34 au COD pour le doré jaune et possiblement pour le touladi et la perchaude. Le taux de croissance
35 juvénile était négativement relié au COD pour le doré jaune et le touladi mais pas pour la
36 perchaude. Ces résultats supportent un nombre croissant d'études suggérant que la productivité
37 des populations de poisson pourrait être liée négativement à la concentration de COD dans les
38 lacs.

39 **Mots clés :** carbone organique dissous, matière organique allochtone, poisson, chaîne
40 alimentaire, productivité

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Introduction

The factors that influence the potential productivity of inland fisheries are of substantial basic and applied interest. Successful and widely-used fisheries productivity models for lakes have identified factors such as nutrient availability, mean depth, availability of oxygenated habitat, and others as predictors of the productivity of one or many species (Christie and Regier 1988; Leach et al. 1987; Lester et al. 2004; Ryder 1965). These models have been successful in part because they have built from first-principles understanding of the connections between fish ecology and limnological conditions. While limnologists have long focused on nutrients as the primary regulator of lake productivity, dissolved organic matter (usually measured as dissolved organic carbon, DOC) is increasingly recognized as a major control on productivity in many settings (Jones 1992; Prairie 2008; Solomon et al. 2015; Williamson et al. 1999)

In keeping with this newfound appreciation for the effects of DOC on lake productivity, recent work has demonstrated negative relationships between DOC concentrations and the abundance of several fishes in Scandinavian lakes (Finstad et al. 2014; Karlsson et al. 2009). Whereas nutrients have often been a useful predictor of fish production because more nutrients means greater productivity of the food webs that support fishes, DOC seem to be a useful predictor for the opposite reason – high DOC concentrations are associated with lower food web productivity (Jones et al. 2012; Kelly et al. 2014; Solomon et al. 2015). In particular, the availability of zoobenthic prey seems to be the key mechanistic link between DOC concentration and fish biomass (Karlsson et al. 2009). Lakes with higher DOC concentrations have lower zoobenthos biomass (Craig et al. 2015; Karlsson et al. 2009). This may be because the negative effects of DOC on light penetration and thereby on benthic primary production reduce the resource base

available to zoobenthos (Ask et al. 2009; Godwin et al. 2014; Karlsson et al. 2009), or because DOC's effect on stratification depth and thereby on dissolved oxygen concentrations imposes physiological constraints on zoobenthos productivity (Craig et al. 2015). Regardless, because zoobenthos are, directly or indirectly, the primary prey for most fishes in most lakes (Vander Zanden and Vadeboncoeur 2002), the negative effect of DOC on zoobenthos seems to impose an important resource limitation on fish populations.

In this study our objective was to test whether the abundance and growth rate of three common North American fish species, all of which rely on benthic food chains during at least a portion of their ontogeny, were negatively related to lake DOC concentration. We reasoned that if DOC imposes resource limitations on fish populations by reducing zoobenthos productivity, this might affect growth rates in addition to (or instead of) the abundance effects that previous studies have identified. We asked whether DOC was an important predictor of abundance and growth in regression models that also considered other predictors such as total phosphorus (an indicator of lake productivity) and latitude (an indicator of water temperature and distributional patterns). Our results extend understanding of the linkages between DOC concentrations and fish productivity, and provide insights into the potential implications for fisheries management of spatial variability and ongoing temporal change in lake DOC concentrations (Hanson et al. 2007; Monteith et al. 2007).

Methods

Data sources and lake selection

We used our own sampling and existing unpublished data to assemble abundance and growth rate estimates across wide DOC gradients for walleye (*Sander vitreum*), lake trout (*Salvelinus namaycush*), and yellow perch (*Perca flavescens*). Data for walleye and lake trout came from Québec's Ministère des Forêts, de la Faune et des Parcs (MFFP; 74 walleye lakes and 154 lake trout lakes in the initial data set; see details below). From their database we identified potential focal lakes as those in the southern portion of the province for which there was adequate length-age data to permit good growth rate estimates. We then used an existing lake chemistry database to select lakes from this list spanning the widest possible DOC gradient. We also considered travel logistics in our final selection of lakes, because our goal was to collect our own water chemistry samples from each lake to minimize potential methodological variation in estimates of chemical predictors in our regression models. For yellow perch, data were from our own sampling efforts during May to August 2013. We identified probable yellow perch lakes in the southern portion of the province based on the MFFP's database (which indicated presence of this species), and again used the chemical database to pick lakes across a wide DOC gradient, and travel logistics. Some lakes sampled for perch were also included in our walleye or lake trout data sets.

Lake characteristics

We measured mixed layer DOC and TP concentrations on a pooled water sample (top, middle, and bottom of mixed layer) collected with a Van Dorn bottle near the deepest point of each lake. DOC samples were filtered through 0.7 µm glass microfiber filters and analyzed on an Aurora 1030W TOC Analyzer. TP samples were analyzed by measuring absorbance at 890 nm after persulfate digestion (Murphy and Riley 1962; Wetzel 2001). Sampling was conducted between

May and August 2013 for most lakes, but for 18 lakes we used DOC and TP measurements that had been made previously using similar methods (Table S1).

Fish sampling, abundance, and growth rate

Abundance and length-age data for walleye and lake trout came from standardized surveys conducted by Québec's MFFP between 1988 and 2012. Experimental gill nets composed of eight 7.6 m by 1.8 m panels ranging from 25 to 152 mm stretch mesh were set perpendicular to shore and fished overnight (including at least the period from 18:00 to 09:00) for 18-24 hours. For walleye, sampling was conducted in autumn and nets were set at depths between 0 and 15 m. For lake trout, sampling was conducted in late summer and nets were set at depths corresponding to preferred habitat in each lake ($< 12^{\circ}\text{C}$ and $> 5\text{ mg L}^{-1}$ dissolved oxygen), but not deeper than 40 m. Total effort for each lake-year sampled varied depending on lake surface area, from 4 net-nights in lakes $< 200\text{ ha}$ to 48 net-nights in lakes $> 10,000\text{ ha}$ for walleye, and from 5 net-nights in lakes $< 150\text{ ha}$ to 50 net-nights in lakes $> 5,000\text{ ha}$ for lake trout. In some cases additional nets were set to target particular species or size classes; these sets were excluded from calculations of abundance but included in length-age data sets. Complete details of these methods are provided by Service de la Faune Aquatique (2011).

We used similar methods to collect yellow perch between May and August 2013. Experimental gill nets composed of four 7.6 m by 2.4 m panels ranging from 38 to 89 mm stretch mesh were set perpendicular to shore and fished overnight (including at least the period from 19:00 to 05:00) for 12 to 16 hours. Due to restrictions on our collector's permit intended to minimize mortality of coldwater species, the bottom edge of these nets never extended below the

thermocline. Total effort for each lake was 4 net-nights. We also used a beach seine (7.6 m long, 13 mm mesh), minnow traps (25 mm mouth aperture), and a fyke net (6 mm mesh, 18 m wings) to capture additional yellow perch for length-age analysis; captures from these gears were excluded from calculations of abundance. All use of fish in this study was in accordance with our institutional animal care and use protocol.

Total length of captured fish was measured to the nearest millimeter, and mass was measured to the nearest gram using an electronic or spring balance. Sagittal otoliths were extracted from a subset of individuals, sectioned in the transverse plane, and examined under a microscope to determine age. A single reader examined each otolith on two occasions separated by ~3 months, examined the second otolith of any fish for which the two readings did not agree, and discarded from the data set any fish for which the age remained uncertain at that point. The resulting age estimates agreed closely with those from two independent readers who examined a subset of the otoliths. Most of the data in each lake were from fish aged 0 to 11 for walleye, 0 to 14 for lake trout, and 0 to 8 for yellow perch; maximum ages in the data set were 34, 41, and 16 years respectively. We used catch per unit effort (CPUE; individuals * net-night⁻¹) and biomass per unit effort (BPUE; kg wet weight * net-night⁻¹), calculated across all of the standardized gillnet sampling in each lake, as indices of abundance, and used the standard deviation of each index across net-nights to describe the precision of these estimates. To estimate growth rates, we fit the Gallucci and Quinn (1979) parameterization of the von Bertalanffy growth model to the length-age data for each species in each lake:

$$[1] \text{ length} = \frac{\omega}{k} (1 - e^{-k * \text{age}})$$

In this parameterization the ω parameter describes the early growth rate and has units of length per time. We fit this model to the data by maximum likelihood, with a Gamma likelihood. We described the precision of the ω estimates by estimating the standard error of ω from the information matrix (Bolker 2008). We did not distinguish between male and female fish in this analysis, and did not record sex for the yellow perch that we collected (sex ratios for walleye and lake trout are given in Table S1). We reasoned that sexual dimorphism in size at age should have little effect on estimates of early growth rate, because the dimorphism is most pronounced for older fish whereas younger fish provide most of the information that constrains the early growth rate parameter. Indeed, initial analyses demonstrated that there were significant differences between male and female growth rates for only 4 of the 18 walleye lakes and 1 of the 16 lake trout lakes, and that the sex-specific estimates were on average within 14% and 18% of the overall estimate for walleye and lake trout respectively. All statistical analyses were conducted using the R software (2014).

Regression analyses

We fit multiple regression models to the abundance and growth rate data to isolate any effect of DOC while controlling for other potentially important factors. Specifically, we considered latitude, surface area, TP, and DOC as predictors of CPUE and BPUE; and all of these predictors plus CPUE as predictors of growth rates. We used CPUE instead of BPUE as an indicator of abundance in the growth rate models because the average precision (CV) of replicate measures within a lake was slightly better for CPUE than for BPUE for all three species. We also ran but do not present models using BPUE as the abundance predictor; because CPUE and BPUE were strongly correlated, results were similar for these models. We fit models including all possible

combinations of predictors, ranked the models by AICc, and retained models with $\Delta\text{AICc} < 4$. The growth rate estimate for each lake was weighted by the inverse of its variance. All predictors and response variables were log-transformed prior to analysis. To convey visually the relationship between the response variables and DOC in particular, we plotted the response (or the residuals from a regression of the response on an important predictor such as latitude) versus DOC. We also used hierarchical partitioning to estimate the independent effect of each predictor on the response variables (Chevan and Sutherland 1991; Mac Nally 2000).

Results

The lakes in our data set were located between 45.0 and 48.7° N latitude, and ranged in surface area from 20 to 91,000 ha, in TP concentration from 2 to 160 $\mu\text{g L}^{-1}$, and in DOC concentration from 2.6 to 16.0 mg L^{-1} (Table S1). The range of DOC concentrations was wider for walleye and yellow perch lakes (4.3 to 16.0 mg L^{-1} and 4.1 to 15.8 mg L^{-1} , respectively) than for lake trout lakes (2.6 to 8.8 mg L^{-1}). Surface area and DOC concentration were significantly positively correlated with latitude (log-log, $r=0.32$ and $r=0.61$, respectively, $p<0.03$), in part because lakes in the relatively northern Abitibi region tended to be large and have moderate to high DOC concentrations. DOC and TP concentrations were significantly positively correlated (log-log, $r=0.63$, $p<0.0001$). None of the other correlations among latitude, surface area, TP, and DOC were significantly different from zero ($p>0.21$).

Because our walleye and lake trout data often came from multiple samples over multiple years, whereas yellow perch were sampled with a single sampling effort in each lake, the precision of our abundance and early growth rate estimates was generally higher for the first two species than

for perch (Table S1). The standard deviation of CPUE ranged across lakes from 6 to 60% of the mean for walleye (mean=26%), from 2 to 127% of the mean for lake trout (mean=37%), and from 34 to 200% of the mean for yellow perch (mean=90%). These patterns also held for BPUE. Similarly, the number of fish for which length-age data were available was higher for walleye (range 20 to 1,720 individuals, mean=468) and lake trout (range 34 to 818, mean=255) than for yellow perch (range 30 to 57, mean=44). Consequently, estimated early growth rates (ω) were generally well-constrained for walleye and lake trout, but less so for yellow perch. The standard error of ω ranged across lakes from 1 to 8% of the mean for both walleye and lake trout (mean 3-4%), whereas for yellow perch it ranged from 2 to 22% of the mean (mean 7%).

Abundance of walleye, and perhaps also lake trout and yellow perch, was negatively related to DOC concentration (Table 1, Figure 1). We report results using both CPUE and BPUE as the response variable for each species, although these two measures were fairly strongly correlated ($r=0.85$, 0.93 , and 0.90 for walleye, lake trout, and yellow perch respectively; log-log). For walleye, a negative DOC effect appeared in all of the top models for BPUE, and in the best model for CPUE (although other models for CPUE that did not include the DOC term had similar predictive power). For lake trout and yellow perch the DOC effect on BPUE and CPUE was always negative when it appeared in one of the top models, and for yellow perch CPUE the addition of DOC to a model with latitude explained some additional variance, but in general for these two species the DOC effect was described as well or better by alternative predictors like total phosphorus, surface area, or latitude. Latitude was a good predictor of abundance for all three species, and its independent contribution to explaining abundance was larger than that of

DOC or any other predictor. Walleye were more abundant, and lake trout and yellow perch less abundant, in lakes at higher latitudes within our dataset.

Early growth rates were negatively related to DOC concentration for walleye and lake trout, but not for yellow perch (Table 2, Figure 2). For walleye, there was a clear negative relationship between early growth rate and abundance, with CPUE appearing in all of the top models and explaining 23% of the variation in growth rate on its own. An additional ~20% of the variation in walleye early growth rate was describable as a negative relationship with latitude and/or DOC concentration, which were strongly correlated in the walleye lakes ($r=0.77$, log-log). The predictive ability of the DOC and CPUE model was indistinguishable from that of the latitude and CPUE model ($\Delta AICc=0.7$), and a model including both DOC and latitude along with CPUE retained the negative DOC effect and was within the set of plausible models. Latitude made the largest independent contribution to explaining walleye early growth rate (37%), followed by DOC (26%) and CPUE (23%). For lake trout, early growth rate was clearly negatively related to DOC concentration and positively related to TP concentration. The best model included both of these predictors and described 51% of the variation in lake trout early growth rates. In the hierarchical partitioning analysis, DOC made the largest independent contribution to explaining early growth rates for lake trout (48%), followed by latitude (22%) and TP (15%). For yellow perch, early growth rates were uncertain, and not clearly linked to any of the predictors that we considered.

Discussion

Our results suggest that the productivity of several common fish species may be negatively related to DOC concentrations in lakes via decreases in abundance and/or early growth rates. These results are consistent with those described by Karlsson et al. (2009) for Arctic char *Salvelinus alpinus* and Eurasian perch *Perca fluviatilis* in northern Sweden, and by Finstad et al. (2014) for brown trout *Salmo trutta* in Norway, but extend those results in two important ways. First, our results expand the geographic range and set of species for which negative DOC effects on fish productivity have been demonstrated. Second, we show that high DOC concentrations may reduce early growth rates of fishes despite concomitant decreases in abundance that might be expected to yield density-dependent increase in growth.

An important limitation of our study, which it shares with those by Karlsson et al. (2009) and Finstad et al. (2014), is that it is correlative. While correlative studies across natural gradients are a useful and valid method of inference, understanding of the linkages between DOC and fish productivity would be strengthened by complementary inferential approaches such as planned or natural experimental manipulations of DOC concentration.

Two previous studies in the region in which we conducted our work have taken advantage of natural experiments that altered DOC concentrations to look at effects on young-of-year (YOY) yellow perch. In a study of 22 lakes before and after some experienced increases in DOC concentration as the result of logging in their watersheds, Bertolo and Magnan (2007) noted that abundance of young-of-year perch increased with the magnitude of the DOC increase. They interpreted this to be the result of either increased zooplankton productivity or reduced ultraviolet radiation damage on eggs and larvae with DOC increase. Similarly, Leclerc et al.

(2011) observed greater *Daphnia* abundance, higher YOY perch consumption of *Daphnia*, and faster YOY perch growth rates in three lakes where DOC had increased due to logging than in three control lakes.

While these studies focused only on YOY perch, they provide some experimental evidence that DOC can indeed influence fish productivity. Interestingly, both of these studies, as well as another correlative study conducted in northern Ontario (Tanentzap et al. 2014), showed *positive* relationships between DOC and the abundance or growth of YOY perch. Given that YOY perch are largely zooplanktivorous, this perhaps suggests net positive effects of DOC on zooplankton productivity over the DOC ranges considered in these studies. Our own recent whole-lake DOC manipulation experiment showed that modest increases in DOC can increase zooplankton productivity, even where comparative studies across broad DOC gradients demonstrate negative relationships between DOC and zooplankton productivity (Kelly et al. 2014; Zwart et al. 2016; Kelly et al. unpublished manuscript). Furthermore, the results of Finstad et al. (2014) highlight the context-dependence of these patterns, showing that brown trout abundance, while generally negatively related to DOC concentration, is instead positively related in lakes with extremely low DOC.

As this discussion demonstrates, the processes by which DOC influences food web and fish productivity are complex (Solomon et al. 2015; Stasko et al. 2012). Additional manipulative experiments could improve our understanding of these phenomena. Furthermore, future survey-based studies like ours would benefit from increased sampling effort, in terms of the number of fish within a lake (to increase precision of growth and abundance estimates), the number of lakes

sampled across broad environmental gradients (to improve statistical separation of potentially correlated effects), and the number of environmental covariates considered (to distinguish potential mechanisms underlying observed patterns). For example, the strong effects of latitude on abundance and growth rate in our analysis could potentially be due to differences in temperature or to other factors (Venturelli et al. 2010), and other factors like angler harvest and intra-specific competition might also affect abundance and growth. Data from ongoing monitoring efforts by fisheries management agencies could be extremely valuable in this regard, as it was in our own study. Given the limitations of correlative studies, it is notable that DOC consistently emerged as a useful predictor of abundance and growth in our analyses, with the hypothesized negative effect.

A negative effect of DOC on growth and abundance is consistent with the idea that DOC limits fish production by limiting zoobenthos production. All three of the species that we considered rely heavily on zoobenthos, or on fish that eat zoobenthos, as their prey base during most of their ontogeny. For instance, total direct and indirect reliance on zoobenthos, estimated from gut content data, averaged 58% in 20 populations of walleye, 53% in 70 populations of lake trout, and 77% in 90 populations of yellow perch (Vander Zanden and Vadeboncoeur 2002). The differences between species that we observed in the strength of the relationships between DOC and growth and abundance may be linked to differences in their ecology, as we discuss next.

Species-specific responses

High DOC concentrations appear to have particularly strong effects on walleye; both abundance and early growth rate were lower in darker lakes, despite the potential for density-dependent

increases in growth at low abundance. This result fits well with previous work on the determinants of walleye productivity, and suggests some interesting new insights. Walleye rely heavily on benthic food chains and this trophic niche remains fairly constant across broad DOC gradients (Stasko et al. 2015). Because walleye foraging activity is linked to ambient light levels, previous work has used the area of benthic habitat with suitable light levels, along with the temperature preferences of walleye, to predict walleye yield across lakes (Lester et al. 2004). Our results are consistent with that yield model, because high DOC concentrations reduce light penetration and thermocline depth, particularly in smaller lakes (Solomon et al. 2015). On the other hand, the other important predictor in the yield model is total dissolved solids (TDS) (Lester et al. (2004), which serves as an indicator of productivity and is positively related to walleye yield. DOC is a small component of the total dissolved solids, and higher DOC concentrations tend to be associated with greater nutrient concentrations. But evidence from lake surveys and modelling analyses shows that the negative effects of DOC on within-lake primary and secondary productivity, via changes in light availability, thermal structure, and oxygen availability, may outweigh the positive effects of nutrient increases associated with higher DOC (Ask et al. 2009; Craig et al. 2015; Godwin et al. 2014; Jones et al. 2012; Kelly et al. 2014). Our finding that DOC concentration is negatively related to walleye abundance and growth, and is a better predictor of these responses than nutrient (TP) concentration, suggests that examining both DOC and TDS might improve predictions of walleye productivity.

For lake trout we observed a clear DOC effect on early growth rate, but only modest evidence for a DOC effect on abundance. Lake trout may rely heavily on benthic food chains, particularly as juveniles but also as adults foraging in shallow water from fall through spring or in brief forays

above the thermocline during summer (Dolson et al. 2009; Vander Zanden and Vadeboncoeur 2002). In this context a strong link between DOC concentration and early growth makes sense, as higher DOC concentrations could limit zoobenthos productivity. Lake trout abundance, on the other hand, is strongly constrained by the availability of cold and well-oxygenated habitat during the summer (Christie and Regier 1988). While DOC does affect these physical habitat characteristics, as described in the previous paragraph, these effects are modest across the limited DOC range of lake trout lakes in our data set or in general, especially for larger lakes where wind mixing is important (Pérez-Fuentetaja et al. 1999; Read et al. 2012; Schindler and Gunn 2004).

We expected to find a negative effect of DOC on early growth of yellow perch, as we observed for walleye. These two species are ecologically relatively similar, and perch have higher average benthic reliance than walleye (Vander Zanden and Vadeboncoeur 2002). Instead, we observed a strong effect of DOC on perch abundance measured by CPUE, but no effect on growth. There are at least two possible explanations for this unexpected result. First, the lack of growth effect could be linked to the relatively limited data that we had for perch, consisting of relatively few individuals captured in a single year in each lake. In contrast, the estimates for walleye and lake trout were derived from much larger samples and often included data from multiple years. Consequently, the growth rate estimates for perch were less well constrained and did not integrate over year-to-year or cohort-to-cohort variability in growth within a lake (Table S1). The observation that none of the predictors that we considered explained much variability in the perch growth rate estimates is also consistent with this interpretation. Second, it could be that the smaller size of perch relative to walleye, and their greater tendency towards planktivory at small sizes, provides some buffer against the loss of energy-dense benthic prey in high-DOC lakes.

Work on Eurasian perch (*Perca fluviatilis*), for instance, shows that while the diet of fish 100-200 mm long is heavily dominated by benthic invertebrates, greater amounts of zooplankton appear in the diet in years when high density forces fish to forage in the pelagic zone (Persson et al. 2000). Some evidence, however, indicates that zooplankton production is also negatively related to DOC concentration (Kelly et al. 2014), suggesting that a shift to planktivory might not be able to offset the loss of benthic prey in higher-DOC systems. Further work is needed to assess how the strong environmental gradients imposed by DOC affect feeding strategies and energetic budgets of perch and other fishes (Estlander et al. 2015).

Fisheries management and DOC

Our results support a growing body of literature suggesting that the productivity of many fish populations is negatively related to DOC concentrations. Many of the species for which this pattern has been demonstrated support important recreational, subsistence, and commercial fisheries, yet the negative effects of DOC on fish productivity are not typically incorporated into the fisheries models used for management. Incorporating DOC effects into these models might improve our ability to manage these fisheries sustainability, especially given the great heterogeneity of lake DOC concentrations across lake landscapes and ongoing changes in DOC concentrations in some regions (Hanson et al. 2007; Monteith et al. 2007; Solomon et al. 2015). At a more fundamental level, additional work using multiple modes of inference is needed to further elucidate the mechanisms by which DOC effects on fish productivity occur.

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Supplementary information – See supplementary data in Table S1.

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Table 1. Regression models describing among-lake variation in abundance of walleye, lake trout, and yellow perch, using catch per unit effort (CPUE) or biomass per unit effort (BPUE) as abundance indices. Columns give the model rank (based on ΔAICc), the ΔAICc , the proportion of variance explained by the model adjusted for degrees of freedom (i.e. the adjusted R^2), and the parameter estimates for the intercept, latitude, surface area, total phosphorus, and dissolved organic carbon effects appearing in each model. For each species we fit models including all possible combinations of these main effects, and show here all of the models that were within 4 AICc units of the best model. All predictors and the response variable were log-transformed, and coefficients are in transformed units. The independent contribution of each variable, estimated from the hierarchical partitioning analysis, is given as a percentage below the predictor name in each sub-table.

Walleye BPUE (n=21)

Model	ΔAICc	R^2_{adj}	Intercept	Lat (50%)	SA (13%)	TP (5%)	DOC (32%)
1	0.0	0.33	-136	37			-1.8
2	0.8	0.38	-138	38	-0.11		-1.8
3	3.5	0.29	-135	36		-0.02	-1.8

Walleye CPUE (n=21)

Model	ΔAICc	R^2_{adj}	Intercept	Lat (59%)	SA (14%)	TP (4%)	DOC (23%)
1	0.0	0.17	-104	28			-1.1
2	0.2	0.08	-44	12			
3	0.3	NA	2.6				
4	2.1	0.08	-47	13	-0.084		
5	2.2	0.17	-105	29	-0.081		-1.1
6	2.4	<0.01	3.1		-0.068		
7	3.0	<0.01	2.3				0.13
8	3.0	<0.01	2.5			0.026	
9	3.1	0.14	-109	30		0.093	-1.3
10	3.2	0.03	-46	13		-0.045	

Lake trout BPUE (n=29)

Model	ΔAICc	R^2_{adj}	Intercept	Lat (65%)	SA (6%)	TP (20%)	DOC (10%)
1	0.0	0.27	109	-28			
2	1.2	0.28	121	-32	0.13		
3	2.2	0.25	98	-25		0.21	
4	2.7	0.24	107	-28			-0.065
5	3.9	0.25	117	-31	0.14		-0.22
6	4.0	0.25	113	-30	0.12	0.13	

516 Lake trout CPUE (n=29)

Model	$\Delta AICc$	R^2_{adj}	Intercept	Lat (72%)	SA (7%)	TP (12%)	DOC (8%)
1	0.0	0.33	129	-33			
2	2.6	0.31	125	-32	-0.042		
3	2.6	0.31	126	-33			-0.12
4	2.7	0.31	127	-33		0.032	

517

518 Yellow perch BPUE (n=17)

Model	$\Delta AICc$	R^2_{adj}	Intercept	Lat (62%)	SA (4%)	TP (21%)	DOC (13%)
1	0.0	0.37	128	-32			
2	2.8	0.35	114	-29		0.25	
3	2.9	0.35	139	-35	0.11		
4	3.4	0.33	123	-31			-0.17

519

520 Yellow perch CPUE (n=17)

Model	$\Delta AICc$	R^2_{adj}	Intercept	Lat (43%)	SA (2%)	TP (16%)	DOC (38%)
1	0.0	0.28	106	-28			
2	1.6	0.31	84	-22			-0.90
3	2.0	0.30	0.98			0.57	-1.67
4	2.2	0.18	2.1				-1.5
5	3.3	0.24	98	-26		0.14	
6	3.4	0.23	110	-29	0.042		
7	3.7	NA	-1.1				

521

522

Table 2. Regression models describing among-lake variation in early growth rates (ω ; Eq. 1) of walleye, lake trout, and yellow perch. Columns give the model rank (based on ΔAICc), the ΔAICc , the proportion of variance explained by the model adjusted for degrees of freedom (i.e. the adjusted R^2), and the parameter estimates for the intercept, latitude, surface area, total phosphorus, dissolved organic carbon, and catch-per-unit-effort effects appearing in each model. For each species we fit models including all possible combinations of these main effects, and show here all of the models that were within 4 AICc units of the best model. All predictors and the response variable were log-transformed, and coefficients are in transformed units. The independent contribution of each variable, estimated from the hierarchical partitioning analysis, is given as a percentage below the predictor name in each sub-table.

Walleye (n=18)

Model	ΔAICc	R^2_{adj}	Intercept	Lat (37%)	Area (4%)	TP (9%)	DOC (26%)	CPUE (23%)
1	0	0.43	61	-14				-0.31
2	0.7	0.41	7.1				-0.51	-0.33
3	3.2	0.23	5.9					-0.32
4	3.8	0.39	49	-11			-0.13	-0.32
5	3.9	0.39	62	-14	0.011			-0.29
6	3.9	0.39	64	-15		0.020		-0.31
7	3.9	0.39	7.3			0.090	-0.68	-0.33

Lake trout (n=16)

Model	ΔAICc	R^2_{adj}	Intercept	Lat (22%)	Area (7%)	TP (15%)	DOC (48%)	CPUE (8%)
1	0	0.51	5.0			0.16	-0.38	
2	1.6	0.55	-16	5.4		0.25	-0.61	
3	1.9	0.36	5.4				-0.49	
4	3.0	0.31	4.3			0.21		
5	3.5	0.49	5.0			0.18	-0.42	-0.031

Yellow perch (n=17)

Model	ΔAICc	R^2_{adj}	Intercept	Lat (12%)	Area (28%)	TP (24%)	DOC (12%)	CPUE (24%)
1	0.0		4.4					
2	0.5	0.08	4.2		0.040			
3	1.9	<0.01	4.4					-0.038
4	2.5	<0.01	4.5			-0.043		
5	2.9	<0.01	4.5				-0.040	
6	3.0	<0.01	4.1	0.077				

Figure captions

Figure 1. Relationship between abundance and dissolved organic carbon concentration (DOC) for three fish species in Quebec lakes. The left column shows abundance as catch per unit effort (CPUE) and the right column uses biomass per unit effort (BPUE). Abundances are plotted as the residuals from regressions of each abundance index on latitude, which was an important predictor of abundance for all species and both indices (see Table 1).

Figure 2. Relationship between early growth rate and dissolved organic carbon concentration for three fish species in Quebec lakes. Data are residuals from regressions of early growth rate on abundance (for walleye) or on total phosphorus concentration (for lake trout), because these were identified as important predictors of growth rate for these species (see Table 2).

Early growth rate, ω (mm y^{-1}) or growth rate residuals

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