Influence of dissolved organic carbon (DOC) on fish production in north-temperate lakes.

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Abstract

Terrestrial inputs of dissolved organic carbon (DOC) can have strong effects on the physical, chemical and biological characteristics of lake ecosystems which can in turn be reflected by changes in production of aquatic organisms. The first chapter of this thesis described the interconnections between aquatic and terrestrial ecosystems and reviewed the different mechanisms through which variable inputs of terrestrial organic carbon could influence fish community dynamics in freshwater environments, and how these effects could be related to changes in fish production. The second chapter evaluated if growth and relative abundance/biomass of three common North American fish species: yellow perch (*Perca flavescens*), walleye (*Sander vitreus*), and lake trout (*Salvelinus namaycush*) are negatively, positively or not correlated with variable DOC concentration and how this relation varies between species. In general, our results provide only limited support of a possible relation between fish production and DOC concentration. Walleye growth rates declined by 50 % across a DOC range from 4.6 to 16.0 mg·l^{-1} but no relation were observed for yellow perch across a DOC range from 4.1 to 15.7 mg·l^{-1}. Variable reductions in walleye growth and yellow perch relative abundance/biomass were observed along with increases of DOC concentration. Increases in lake trout production were not related to DOC (ranging from 2.6 to 8.8 mg·l^{-1}), but strongly related to higher total phosphorus (TP) concentration and to some extent, lower latitude. Hence, the importance of the DOC-growth relation was not consistent between each fish species included in our analysis, suggesting that a species-specific approach should be prioritized over a more general approach when evaluating the possible effect of changes in DOC concentration on freshwater fish production.

Résumé

Les apports terrestres en carbone organique dissous (COD) peuvent fortement modifier la productivité et les caractéristiques des écosystèmes lacustres, avec des répercussions potentielles sur les communautés de poissons. Le premier chapitre de cette thèse décrit l'inter-connectivité entre les écosystèmes aquatiques et terrestres, en présentant les différents mécanismes par lesquels une variation des apports en carbone organique du milieu terrestre pourrait influencer la dynamique des communautés de poissons d'eau douce et comment de tels changements pourraient être liés à une variation de la production de poisson. Le second chapitre évalue si la croissance et l'abondance/biomasse relative de trois espèces de poissons communes en Amérique du Nord : la perchaude (*Perca flavescens*), le doré jaune (*Sander vitreus*) et le touladi (*Salvelinus namaycush*) sont négativement, positivement ou non corrélés avec la concentration en COD et si l'importance de la relation varie entre les espèces. En façon générale, nos résultats fournissent un support limité pour l'hypothèse d'une relation entre la productivité de poisson et la concentration en COD. Le taux de croissance du doré jaune a diminué de 50 % au travers d'un écart de DOC allant de 4.6 à 16.0 mg·l^{-1} mais aucune relation n'a été observée pour la perchaude dans un écart de DOC allant de 4.1 à 15.7 mg·l^{-1}. Des réductions importantes de croissance pour le doré jaune et d'abondance/biomasse relative pour la perchaude ont été observées avec l'augmentation de la concentration en COD. L'augmentation de la production de touladi n'était pas relié au DOC mais était plutôt fortement reliée à des concentrations plus élevés en phosphore total (PT) et jusqu'à un certain point, à des latitudes plus faibles. Ainsi, l'importance de la relation COD-croissance n'était pas consistante entre les espèces de poisson incluses dans notre analyse, suggérant qu'une approche spécifique à l'espèce devrait être priorisée par rapport à une approche plus générale lors de l'évaluation de l'effet possible d'une variation de la concentration en COD sur la production des populations de poisson.

Contributions of Authors

This thesis consists of a two chapters: a general literature review (Chapter I) and a manuscript intended for publication (Chapter II). The original research ideas and sampling methodologies were developed by the candidate and his supervisor. The candidate was also responsible for obtaining data from management and conservation agencies in addition to data collection, management, analysis, and writing the initial drafts of the manuscript to be published and the thesis.

As the supervisor, Christopher T. Solomon provided guidance and support during these two years of preparation, field work, analysis, interpretation and writing. As the co-supervisor, Beatrix E. Beisner helped in obtaining data and provided useful comments and ideas through the development of this project. The manuscript is co-authored by both the supervisor and co-supervisor.

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General introduction

In nature, organisms have evolved a great variety of life history traits (*e.g.* age and size at maturity, size at birth, mortality and survival rate, number and size of offspring, growth rate etc.) that direct shape population dynamics by their effects on survival and reproduction (Cole 1954; Stearn 1976; Roff 1992). A well-documented example is the association between clutch and egg size and offspring survival in birds (*e.g.* Wiebe and Brotolotti 1995). In fish, a rapid evolution in both morphology and life histories traits has been observed when populations are exposed to different selective pressures (Roff 1992). These selective pressures that varies for different environments have been leading to important changes in both the phenotypes and genotypes of fish species (Roff 1992; Haugen and Vøllestad, 2001). It is common to observe variation in intraspecific life history traits among fish species (Roff 1992) and this variation has been associated with differences in both abiotic and biotic factors such as food availability (Vander Zanden and Vadeboncoeur 2002), predation rate (O'Gorman and Burnett 2001), temperature (Huff et al. 2004), fishing pressure (Conover and Munch 2002) and the physical habitat (Stasko et al. 2012).

In the quest to identify what variables influence production and community structure in north-temperate lakes, dissolved organic carbon (DOC) is receiving more and more interest from limnologists; publications related to the subject have been increasing exponentially since the 1980's (Prairie 2008). Indeed, the importance of terrestrial organic matter inputs in lakes and the terrestrial-aquatic linkages represented by the different impacts of DOC has been discussed at many levels (Jones 1992; Schindler and Gunn 2004; Karlsson et al. 2009; Jones et al., 2012; Finstad et al., 2014).

Recent studies have indicated that a reduction in fish production could be observed along with increases of terrestrial organic matter inputs in lakes (Karlsson et al. 2009; Finstad et al. 2014). However, little is known regarding the possible mechanisms explaining this variation in production, including the proportion of the variation in fish growth rate related to these changes in DOC concentration.

Research objectives

In this thesis, I identify the possible influence of changing dissolved organic carbon on fish production in north-temperate lakes. In the first chapter, I present a review of the multiple effects that DOC can have on lake characteristics, and the associated implications on fish communities. In the second chapter, I compare the early life growth pattern of different fish populations (hereafter referred as "population early growth rates") for three common North American fish species which have evolved in a wide range of DOC concentrations in order to investigate how changes in DOC concentration could impacts fish growth and if the DOC-fish growth relation can vary for different fish species.

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Chapter 1: Possible effects of variable DOC concentration on fish communities

Much research has been conducted to evaluate what causes the spatial and temporal variation in terrestrial organic matter inputs in freshwater ecosystems (*e.g.* Read and Rose 2013), and what could be the possible implications of changes in climate (*e.g.* Magnuson et al. 1997; Tranvik et al. 2009) and higher anthropogenic perturbations (St-Onge and Magnan 2000; Bertolo and Magnan 2007; Leclerc et al. 2011) on dissolved organic carbon levels. Considering the far reaching effects that DOC has on aquatic ecosystems, and the potential implications that variable DOC could have on fish production, there is a need to better measure and understand these effects. In this chapter, I will review 1) the main drivers of the variation in DOC concentration in freshwater ecosystems, 2) the implications for fish communities, 3) the effects of DOC-driven changes on lake production and finally, 4) the impacts of a reduction in water clarity on fish communities.

1. Interconnections between aquatic and terrestrial ecosystems

Aquatic and terrestrial ecosystems are linked by water and material moved in groundwater and surface water from the drainage basin to recipient lakes and rivers. During the transition, multiple chemical and biological reactions modify the quality and quantity of nutrients and organic substances (Wetzel 2001). Because it is strongly influenced by the surrounding area, it is now commonly accepted that lake ecosystems are represented by both the lake and its entire drainage basin. Nearly all of the organic matter found in the aquatic ecosystems consists of dissolved organic carbon (DOC) and particulate organic carbon (POC) (Wetzel 2001). In lakes, DOC alone represents the largest reservoir of organic carbon in the water column, followed by heterotrophic bacteria that are estimated to be 40 times smaller (Prairie 2008). Two major sources of DOC are generally considered in lake ecosystems: autochthonous production by autotrophic organisms including phytoplankton, benthic algae and macrophytes (Bertilsson and Jones 2003) and allochthonous inputs of terrestrial material

(Aitkenhead-Peterson et al. 2003). Of the two, allochthonous DOC which comes from decomposing vegetation in wetlands and forest soils represents the main contribution (Schindler and Gunn 2004; Bade et al. 2007).

Inputs of terrestrial organic matter are influenced by many different factors such as catchment size, vegetation composition and density, presence of wetland, air temperature, runoff, precipitation and UV radiation (Wetzel 2001; Tranvik and Jansson 2002; Schindler and Gunn 2004; Karlsson et al. 2009). Because terrestrial DOC is continuously processed in the soil before reaching aquatic systems, it is relatively recalcitrant to further decomposition (Schiff et al. 1997) and has a high molecular weight and a complex chemical structure (Jones 1992), being composed mainly of fulvic, humic and tannic acids (McKnight and Aiken 1998; Schindler and Gunn 2004). These compounds absorb light in the violet region of the spectrum, giving water a yellow-brown color reminiscent of tea (Cuthbert and del Giorgio 1992; Schindler and Gunn 2004).

DOC concentration is now considered as a fundamental variable controlling lake structure and function and it is receiving more and more interest from limnologists (Prairie 2008). Two main properties can explain the importance of DOC effects on lake ecosystems; 1) its coloration and associated light attenuation capacity that changes the vertical light and heat distribution in lakes (Kirk 1994; Fee et al. 1996) and 2) its contribution to the basal resource availability (energetic input to the base of the lake food web) and subsequent production for higher trophic levels (Tranvik 1988; Pace et al. 2004; Carpenter et al. 2005; Solomon et al. 2011). Given these characteristics, variable DOC concentration can have diverse and powerful impacts on physical, chemical and biological aspects of lakes (Jones 1992; Schindler and Gunn 2004; Pace and Cole 2004). Figure 1 represents a summary of DOC characteristics, allowing to easily understand the complexity of its role in aquatic ecosystems and how it can be linked to each aspects of lakes.

2. Possible implications of DOC for fish communities

The relative importance of the different environmental stressors that can influence fish communities in north-temperate regions vary between lakes, species and even different life stages of the same species. Due to the complexity of species interactions in lake ecosystems and the far-reaching effect that DOC have on the physical, chemical and biological properties of fish habitat, evaluating the possible implications of variable DOC concentration on fish communities can be challenging. This complexity can be better visualized through a concept map of the possible interactions that are linking the allochthonous inputs of carbon to fish communities in lakes (figure 2).

The potential effects of DOC on fish communities can be appreciated in a simplified way with Hutchinson's ecological niche concept (Hutchinson 1944), involving habitats composed of physical and biological gradients that change over time. With this concept, the habitat limits for a given species are influenced by its physiological and behavioral limits and by environmental parameters (physical and biotic). Since many physical and biotic factors are interacting, only a smaller portion of the fundamental niche is occupied by a species (referred to as the realized niche) (Hutchinson 1978). In north-temperate lakes, DOC represent one of these environmental parameters and both the direct and indirect effects of DOC added to the species-specific optimal growth and reproduction conditions are influencing the size of each species realized niche.

3. Light attenuation effect on fish communities

The influence of DOC on the vertical light environment affects multiple important chemical, biological and physical processes in freshwater lakes, including temperature, oxygen and light profile (Stasko et al. 2012). These modifications imply important changes for fish habitat characteristics and thus, the light attenuation effect of DOC is often mentioned when describing its essential role in structuring fish community dynamics. Because the different biotic and abiotic variables that can represent potential predictors of production in aquatic ecosystems are often strongly related, it can be

difficult to distinguish between the simultaneous direct and indirect effects of DOC and associated implications for fish communities.

Light, water temperature, oxygen and habitat volume

The altered lake thermal structure is probably the most obvious and important effect caused by variable DOC concentration (Stasko et al. 2012; Read and Rose 2013). Like most ectothermic organisms, the ambient temperature in fish habitat is a predictor of the length of their growth season, and also has a direct impact on their growth and developmental rates (Atkinson 1994). As a consequence, fish actively seek areas of species-specific preferred temperatures within their environment in order to optimize physiological processes (Fry 1947; Magnuson and De Stasio 1996) which bring us back to the Hutchinson concept presented earlier.

Due to the strong light absorption capacity of DOC, the depth at which solar energy can penetrate in the water column is reduced in darker lakes with higher DOC concentrations (Kirk 1994; Fee et al. 1996). Fee et al. (1996) found that water mixing depths were best identified using extinction coefficients (converted to percentage of transmission), which principally are functions of DOC, except in eutrophic lakes where algal levels are high. In this study, mean midsummer mixing depths ranged from over 13 meters in largest lakes (> 500 ha) to only 2 meters in smallest one (< 500 ha). In the smaller lakes, a faster absorption of light with depth caused by increases in DOC concentration causes the thermocline to be shallower and consequently, reduces the size of the epilimnion (Fee et *al.* 1996; Houser 2006; Read and Rose, 2013) and increases the volume of the colder, less oxygenated hypolimnion (Schindler et al. 1996; Wetzel 2001; Houser 2006). To estimate the implications of a modified stratification pattern, it is essential to consider the associated changes in oxygen availability. Oxygen concentration is an important determinant of the optimal habitat volume available for fish while strongly influencing their survival, growth and reproduction (Scott and Crossman 1973). Because oxygen concentration is also linked to water temperature and stratification pattern in lakes, DOC inputs thus have consequences on fish communities

via both direct temperature effects on growth and reproduction, but also by controlling the habitat availability that is limited by oxygen concentration and temperature (Stasko et al. 2012).

Defining the available habitat for cold-water fish species such as lake trout shows the importance of considering the oxygen concentration in deeper zones. Lake trout are adapted to the deep, cold waters of oligotrophic lakes (Shuter et al. 1998) and have a metabolism that allows movement and growth at low temperatures (Gunn and Pitblado 2004). For example, lake trout optimal habitat has been defined by an upper boundary corresponding to temperatures of less than 10 ˚C and a lower boundary corresponding to O_2 concentrations greater than 6 mg·l^{-1} (Evans et al. 1991). Although cold-water fish species could benefit from accessing a larger volume of cold water in the hypolimnion, the earlier stratification caused by a fast warming of surface waters in darker lakes and the associated prolonged periods of stratification may extend the period of oxygen depletion in this habitat (Stefan et al. 1996; Magnuson et al. 1997). These species may then have to deal with the energetic costs of making excursions into suboptimal thermal habitat in order to reach higher oxygen concentrations (Brandt et al. 2011).

Dillon et al. (2003) mentioned that in some instances, the change in conditions controlling the upper and lower habitat boundaries for cold-water species may have counteracting effects on the resulting optimal habitat volume. For example, increasing nutrient levels (TP) associated with DOC loads can increase oxygen deficits near the bottom (Molot et al. 1992) resulting in a shallower lower boundary for optimal habitat (Dillon et al. 2003). The same change in TP may extend the optimal habitat by its effect on the upper boundary, with shallower Secchi depth associated with increased chlorophyll a concentration (Dillon et al. 2003). However, water clarity in the more oxygenated, colder and deeper oligotrophic lakes associated to cold-water species is generally controlled by DOC rather than TP (Schindler and Gunn 2004), so the effects on nutrient levels will be largely transmitted through the decrease in the lower oxygen

boundary rather than the increase in the upper temperature boundary (Dillon et al. 2003).

For warm-water species such as walleye, yellow perch and bass, an optimal habitat similar to the one described for lake trout by Clark et al. (2004) has been proposed by Lester et al. (2004).In this study, the evaluation of the optimal habitat was constrained by specific ranges in light (Scherer 1976) and temperature (Rose et al. 1999) proposed as favorable for walleye. Further findings from this study also propose that changes in turbidity, lake shape and morphometry are more likely to cause changes in the optimal habitat and thus, optimal resources available. The definition of optimal resource differs strongly between cold-water and warm-water species, but also for different warm-water fish species (Vander Zanden and Vadeboncoeur 2002).

Variable optimal habitat caused by changes in light, temperature and oxygen can have important consequences for fish assemblages (Christensen et al. 1996) in terms of growth and productive capacity (Christie and Regier 1988; Lester et al. 2004; Clark et al. 2004). Similarly for resource availability, these changes could represent a stronger impact for fish species that have more specific habitat needs. Acclimation, phenotypic plasticity (Morbey et al. 2006) and genetic variability (Galarowicz and Wahl 2003) could also explain among-population differences observed when assessing the impacts of changes in thermal and oxygenated habitat due to DOC concentration.

Fish foraging efficiency

Multiple factors can reduce light availability in lakes (*e.g.* dissolved and colloidal organic matter, suspended inorganic particulates and phytoplankton) and the light scattering (turbidity) and absorption (color) effects of a single factor can act independently, resulting in highly variable light attenuation capacities (Koenings and Edmundson 1991). The visibility of a prey item requires the predator to detect a difference in contrast between the prey and the background, which is dependent upon the optical properties of the object, the water clarity parameters that influence optical properties of the

background and the medium (Utne-Palm 2002). In general, darker waters result from the combinations of both higher turbidity and water coloration from terrestrial inputs of dissolved and particulate organic matter, creating lower light intensity and poor image transmission (Aksnes and Utne 1997). This reduced visibility limits visual predator foraging efficiency while enhancing escape opportunities and refuge availability for prey (Aksnes and Utne 1997). Accordingly, previous studies have shown the negative effect of a darker environment for many fish species considered as visual feeders, including bluegill (Vinyard and O'Brien 1976), brook trout (Confer et al. 1978), largemouth bass (Crowl 1989), Chinook salmon (Gregory and Northcote 1993) and two-spotted goby (Utne 1997).

In oligotrophic lakes, light transmission usually shows a strong negative exponential correlation with DOC concentration (Schindler and Gunn 2004; Karlsson et al. 2009). This effect of DOC on light climate could influence predator-prey dynamics and fish foraging strategies by altering visual detection from predators and reaction distance of prey (Vogel and Beauchamp, 1999; Carter et al., 2010). It is important to note that the optimal light intensities for visual foraging varies a lot for different fish species but also between different life stages of the same species depending on eye physiology (Ali et al. 1977; Vandenbyllaardt and Ward 1991; Vogel and Beauchamp 1999). Walleye represent a good example of a fish species that is well adapted to darker, more turbid environments, due to a special visual apparatus, the *tapedum lucidum*, and the presence of macroreceptors that are developed during the first year of life (Ryder 1977; Vandenbyllaardt and Ward 1991; Guzevich 1993). The development of this higher light sensitivity correlates with the change from a planktivore to a piscivore diet (Bulkowski and Meade 1983; Vandenbyllaardt et al. 1991). Changes in the optimal light conditions associated with shifts in foraging strategies have also been observed for bluegill sunfish (*Lepomis macrochirus*) (Hairston et al. 1982). These shifts in feeding behaviours could also result from fish adaptation to suboptimal foraging conditions associated to darker environments while both predator (Dill and Frazer, 1984) and anti-predator (Miner and Stein 1996) foraging decisions are changing along with environmental factors, including

water clarity (Carter et al. 2010). Additionally, Stasko et al. (2012) suggested that altered predator-prey dynamics resulting from changes in water clarity could facilitate the invasion of fish species such as bass or yellow perch where they are not normally found which in turn could contribute to disturbing the existing inter-species relations.

Macrophyte density and diversity

Aquatic plant (macrophyte) diversity and coverage has been positively related to fish diversity and abundance (Minns et al. 1994; Randall et al. 1996; Brazner and Beals 1997; Höök et al. 2001). Macrophytes represent a food source, a refuge from water perturbations and predators for small fish, and shade and cooler temperatures (Savino and Stein 1989; Jude and Pappas 1992; Höök et al. 2001; Lougheed et al. 2001). Because macrophyte density is driven by light transmission through the water column, it could substantially be reduced by an increase in DOC concentration (Squires et al. 2002) with a concomitant negative effect for fish species that rely on macrophytic habitat. DOC could also play a critical role in protecting aquatic plants against exposure to the deleterious effects of ultraviolet radiation (UVR) (Schindler and Curtis 1997). This is the explanation given by Skov et al. (2002) for the contrasting results found in some turbid lakes where a positive relationship between increasing DOC and macrophyte biomass had been observed. In addition, it has been suggested that changes in macrophyte species composition due to changes in light availability can also modify trophic interactions by changing basal resource use by fish and invertebrate prey (Kovalenko and Dibble 2011).

DOC chemistry and fish physiological stress

In addition to the multiple effects that DOC can have on lake physical characteristics, it is also causing important chemical modifications that have predominantly positive impacts for fish populations by reducing some physiological sources of stress. (Stasko et al. 2012).

First, DOC can play an important role in reducing pollutant toxicity for fish. DOC is mostly composed of charged molecules which tend to aggregate and form stable colloids with other charged chemicals, including organic contaminants that

bioaccumulate in fish tissues (Haitzer et al. 1998; 1999; Schindler and Gunn 2004) and trace metals such as aluminium that can precipitate on the gills and interfere with essential ionoregulation and osmoregulation processes (Rosseland and Staurnes 1994; Wood et al. 2011). Additionally, DOC could promote resilience of freshwater fishes to pollutants by directly changing gill membrane permeability and increasing active uptake of sodium (Na^+) that plays a crucial role in ionoregulation and osmoregulation for fish (reviewed in Wood et al. 2011). In this case, DOC is directly acting on gill physiology to counter-act the negative effects of toxicant that inhibits active Na^+ uptake and increase it.

Second, a for macrophytes, DOC can represent a protection against deleterious effects of UVR for aquatic animals by the attenuation of UV light (Schindler et al. 1996; Williamson et al. 1999; Huff et al. 2004). While the importance of the UVR on aquatic organisms differs, a negative effect on zooplankton, phytoplankton, invertebrates and fish predators has previously been observed (Williamson 1995; Huff et al. 2004; Gonçalves et al. 2010). In fish, the exposure to UVR has been associated with slower development of embryos and juveniles for multiple north temperate species such as northern pike (Vehainen et al. 2007) and yellow perch (Huff et al. 2004; Bertolo and Magnan 2007; Boily et al. 2011). For yellow perch, while juveniles can reduce their exposure to UV by regulating their depth, exposure to UV can severely reduce egg survival, hatching success and population relative abundance in lakes with low DOC contents (Huff et al. 2004). The same positive effects of DOC protection against UVR have been observed on fish behavior (Williamson et al. 1999), allowing an increase in surface water foraging throughout the day by planktivorous fish in darker lakes. UVR is generally recognised as an important physiological stressor, and Stasko et al. (2012) mentioned that the predicted increases in DOC concentration in boreal lakes will likely be beneficial for younger fish life stages. However, it is important to keep in mind that it is the humic portion of DOC, composed mainly by humic and fulvic acids, that determines how DOC can impact water coloration but also its capacity to protect against contaminant toxicity (Wood et al. 2011). Thus, depending on its provenance and

composition, different sources of DOC offers different levels of protection (Haitzer et al. 1999).

4. DOC effects on lake production

While terrestrial carbon has important physical and chemical impacts on lake ecosystems, it can also represent a resource for aquatic consumers (Jones et al. 2012). There is strong evidence that organisms involved in the microbial food web of lakes consume terrestrial organic carbon (Tranvik 1988; Kritzberg et al. 2004; Berggren et al. 2010). While bacteria represent the main pathway for the inclusion of terrestrial resources in lake food webs, zooplankton and zoobenthos also appear to incorporate significant amounts of terrestrial carbon (Carpenter et al. 2005; Solomon et al. 2008, 2011). DOC can then contribute to basal resource availability, by having stimulatory influences on bacteria, heterotrophic algae and protozoa; organisms that can rely on DOC as an energy source (Schindler and Gunn 2004; Lennon and Pfaff 2005; Jones et al. 2012). In turn, these supplement production by supplying food for small zooplankton, which in turn feed larger zooplankton and planktivorous fishes that represent an important part of the diet for some piscivorous fish species (Schindler and Gunn 2004). In oligotrophic boreal lakes with large inputs of terrestrial organic carbon, a significant portion of higher consumer biomass can be derived from allochthonous sources of carbon (Solomon et al. 2011).

On the other hand, a reduction of photosynthetic active radiation (PAR) availability by DOC could restrict the algal production to shallower depths which may have repercussions on higher trophic levels through a decrease in primary production (Vadeboncoeur et al. 2008; Karlsson et al. 2009; Finstad et al. 2014). In oligotrophic north-temperate lakes, increasing DOC concentrations and the associated light attenuation effect act as a strong inhibitor of primary production in the benthic habitat, which represents the main contribution of new biomass in these lakes (Kalsson et al. 2009). Karlsson et al. (2009) found that the reduction in benthic primary production caused by reduced PAR explained a reduction in fish production. It has been argued that

the increases in pelagic autochthonous organic carbon and terrestrial allochthonous organic carbon sources use by fish could not compensate for the loss in benthic primary production in darker lakes (Karlsson et al. 2009).

Conclusion

While some apprehend future increases in DOC concentrations in north temperate lakes (Stasko et al. 2012; Magnuson et al. 1997), more uncertainty has recently been suggested. The far-reaching effects that DOC has on resource availability, lake optical properties and thermal structure makes it a primary factor to consider when listing the possible variables that can explain the changes in fish production. Although, there is added complexity due to interdependence of these effects and variation due to fish species and life-stages, making it difficult to assess the overall impact of changing DOC on fish production. Few studies evaluated how the production of specific fish species is affected by different DOC concentration and to our knowledge, none presented a multi-species comparison of the fish production-DOC relation. Considering this, there is a great need to better evaluate how variable DOC is linked to fish production and if this relation could differ between fish species.

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Fig. 1 Conceptual map of the dissolved organic carbon properties and the possible influence on freshwater ecosystems.
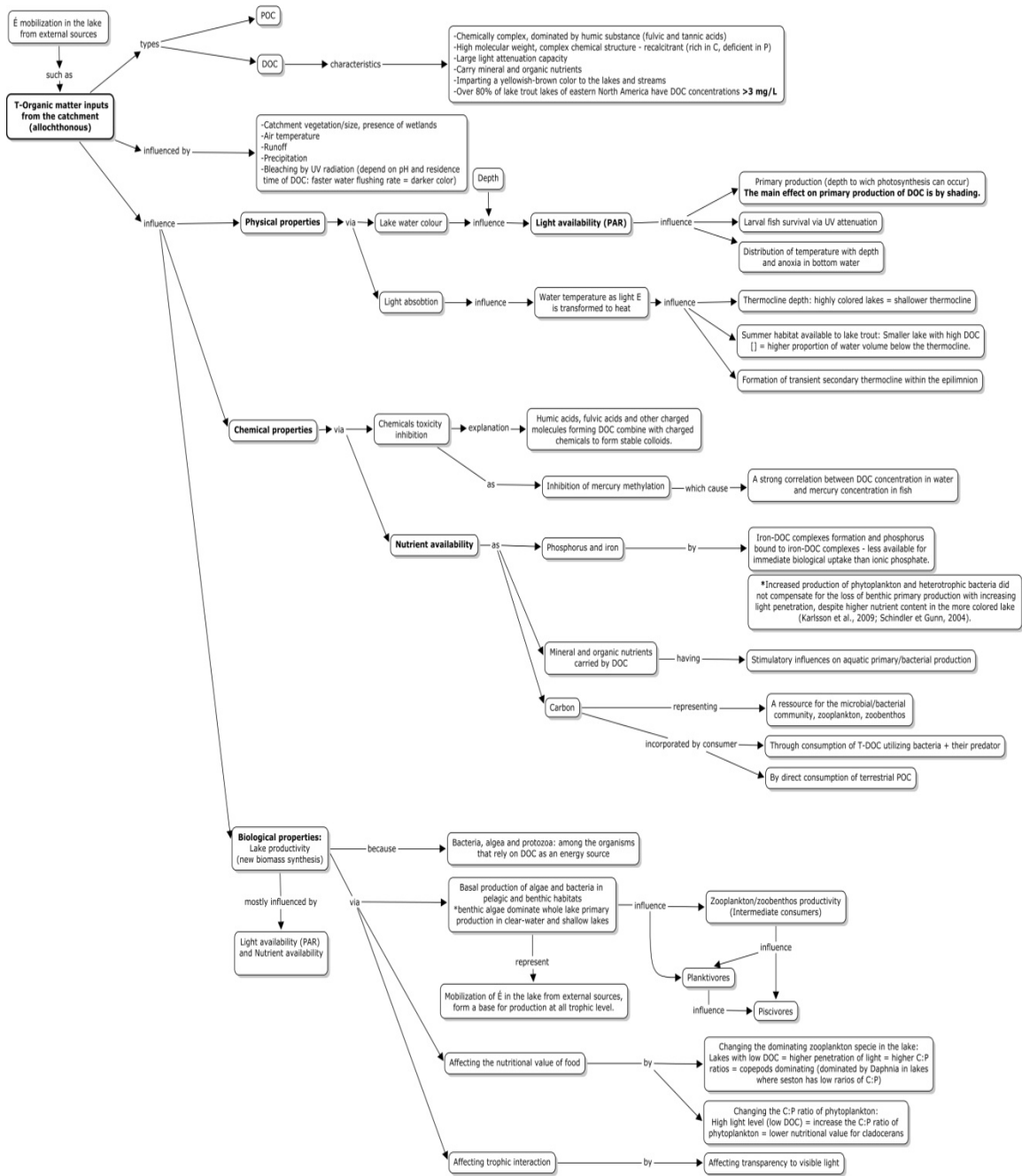
Fig. 2 Conceptual map of the possible influences of terrestrial inputs of organic carbon on fish communities in freshwater ecosystems.
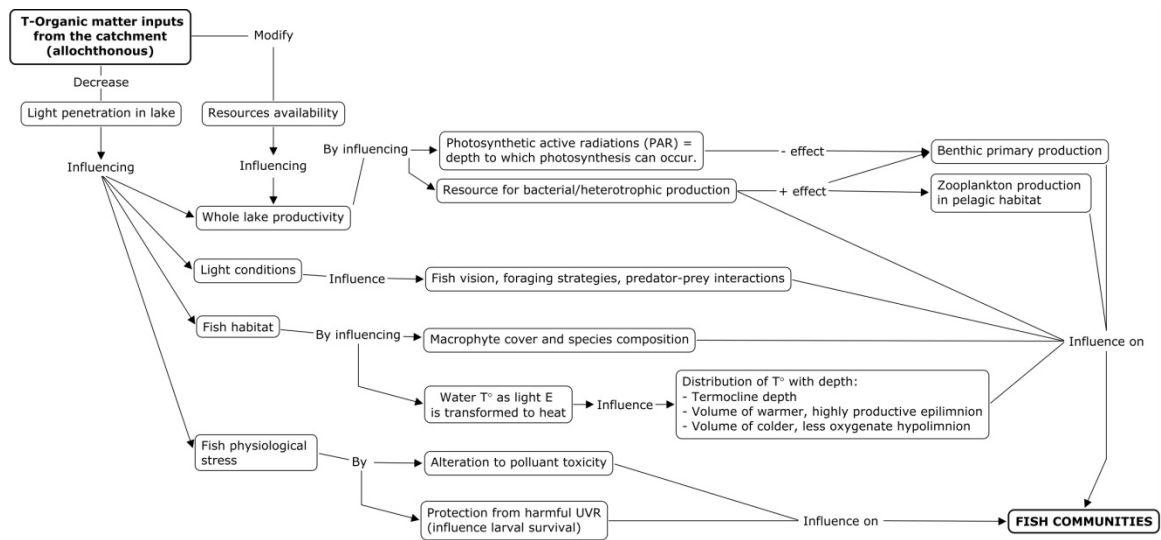
Connecting Statement

The previous chapter establishes the possible pathways by which DOC can change aquatic ecosystem characteristics and possibly affect the production of fish communities. The next chapter aims to verify the relation between changes in DOC concentration and fish production, with a primary focus on growth. Specifically, it examines how fish growth and abundance of three common North American fish species respond to a spatial variation in DOC, and how the fish production-DOC relation differs between species.

Chapter II: Influence of dissolved organic carbon (DOC) on growth of three fish species in north-temperate lakes.

Abstract

Changing inputs of terrestrial dissolved organic carbon (DOC) can have strong effects on the productivity of lake ecosystems in north-temperate regions and on the physical habitat for fish, potentially influencing the productivity of fish and fisheries. The goal of this study was to determine if a variable concentration of DOC could be related to changes in fish production, with a main focus on fish growth. To do so, growth data were used to test if growth and relative abundance/biomass of three common North American fish species: yellow perch (*Perca flavescens*), walleye (*Sander vitreus*), and lake trout (*Salvelinus namaycush*) are negatively, positively or not correlated with DOC concentration and if the importance of this relation varies between species. Our results provided only limited support of a possible relation between fish production (growth and abundance) and DOC concentration. Walleye growth rates declined by 50 % across a DOC range from 4.6 to 16.0 mg·l^{-1} but no relation were observed for yellow perch across a DOC range from 4.1 to 15.7 mg·l^{-1}. Variable reductions in walleye and yellow perch relative abundance/biomass were observed along with increasing DOC concentration. Increases in lake trout production were not related to DOC (ranging from 2.6 to 8.8 mg·l^{-1}), but strongly related to higher total phosphorus (TP) concentration and to some extent, lower latitude. Hence, the importance of the DOC-growth relation was not consistent between each fish species included in our analysis, suggesting that a species-specific approach should be prioritized over a more general approach when evaluating the possible effect of changes in DOC concentration on freshwater fish production.

Introduction

In the last two decades, there has been growing interest from limnologists in assessing the possible implications of terrestrial-derived dissolved organic carbon (DOC) on aquatic ecosystems (Prairie 2008). DOC is now considered as a major regulator among

the fundamental variables that control freshwater ecosystem structure and function, and its possible impacts has been discussed at many levels (e.g. Jones 1992 and Kelly et al. 2014 on plankton; Schindler and Gunn 2004 and Finstad et al. 2014 on fish; Prairie 2008 on the importance of terrestrial carbon in limnology; Karlsson et al. 2009 on lake productivity; Craig et al. *in review* on benthic production).

Given its origin and composition, DOC imposes diverse and powerful impacts on physical, chemical and biological aspects of lakes (Jones 1992; Schindler and Gunn 2004; Pace and Cole 2004). Allochthonous sources of organic carbon from decomposing vegetation in wetlands and forest soil represent the main source of DOC in lakes (Schindler and Gunn 2004). Humic and fulvic compounds compose a large portion of these inputs and gives water a darker, tea-coloured aspect that influences light penetration and heat distribution in the water column by absorbing and reflecting solar energy (Cuthbert and del Giorgio 1992; Jones 1992; Ask et al. 2009). DOC also represents an energetic input to the base of the food web (del Giogio and Peters 1994; Solomon et al. 2011) and can become available to higher consumers like zooplankton and fishes through the bacterial loop (Solomon et al. 2011).

Over the past several decades, terrestrial carbon loads and DOC concentration in water have increased in many north temperate and boreal lakes and is likely to continue to increase in the coming years (Evans et al. 2005; Monteith et al. 2007; Clark et al. 2004). Considering the strong carbon-driven modifications of lake ecosystems characteristics and the potential repercussions on fish habitat, these changes in DOC concentration in north temperate lakes are expected to impact fish production. Although, the directionality and consistency of responses among species are difficult to predict. If changes in DOC concentration could significantly reduce the production of some important fish species, DOC increases could have important socio-economic repercussions on recreational fisheries in North-America.

Recent studies focusing on fish production have demonstrated that indices of fish production are negatively correlated with increasing DOC concentrations (Karlsson et al.

2009; Finstad et al., 2014). The proposed mechanism for this correlation is a negative relation between DOC concentration in lakes and benthic primary and secondary production, which are significantly supporting production of many fish at one of more life stages. Karlsson et al. (2009) has proposed light limitation of benthic algae to explain the reduction in zoobenthos and fish production. Craig et al. (*in review*) also confirmed the DOC-zoobenthos relation but suggested that it has more to do with temperature and dissolved oxygen changes in the water column, not light limitation of primary production. Furthermore, it appeared that the reduction in production (negative correlation) could be observed after DOC concentration is reaching a certain level, situated between 8.0 and 10.0 mg·l^{-1} (Kelly et al. 2014; Craig et al. *in review*).

In general, fish can have a high reliance on zoobenthic prey (Vander Zanden and Vadeboncoeur 2002; Weidel et al. 2008) and the reduction in availability of zoobenthos in high DOC lakes is likely to increase competition for consumers that rely on this resource. This increased competition might influence fish populations either by reducing growth rates or relative abundance (or a combination of both) of the competing species in proportion to their dependence on zoobenthic prey. In all cases, a variation in DOC could result in important changes in fish production. There is little information available on the possible implications of variable DOC concentration on fish production, and if the response of fish growth and abundance to changes in DOC could vary for different fish species.

In this study, our objective was to test whether early growth rates of three common fish species were negatively related to DOC concentrations in a set of lakes. Our focal species (*i.e*. walleye, lake trout and yellow perch) are all heavily benthivorous at specific periods of their life, and so we hypothesized that DOC-driven differences in zoobenthos abundance would affect their early growth. We also expected that the growth-DOC relationship might vary among these species considering that factors affecting their reliance on zoobenthic prey such as feeding behavior and the timing of ontogenetic changes in diet also present species-specific differences.

Methods

For each fish species, we estimated early growth rates from length-at-age data and related these growth estimates to DOC concentration, population relative abundance and other selected predictors. For walleye and lake trout, we used existing fish data from provincial resource management agencies, coupled with existing and new measurements of physicochemical parameters. For yellow perch, we collected new fish data also coupled with existing or new physicochemical parameters. We used linear regressions to test for DOC effects on growth, along with model selection to identify the best models (with or without DOC) for explaining variation in early growth for each species.

Study area

The study area is located in the southern part of the Quebec province, from the Lower Saint-Lawrence region on the East end to the Abitibi region on the West end, and covered a total of 9 different administrative regions (figure 1). In total, 49 lakes were selected based on the availability of historical fish data, their DOC concentration and accessibility. For each fish species, selected lakes were covering the widest ranges of DOC concentration possible, which is almost the same for yellow perch and walleye but a lot smaller for lake trout. Because both fish data availability and DOC concentration were our main criterion, selected lakes are covering wide ranges in DOC concentration but also span large gradients in physico-chemical characteristics (table 1). The geology, morphology, vegetation and soils of the different regions sampled are heterogeneous and contribute to the variability of these characteristics.

Limnological data

In order to control for other lake variables that represent possible fish growth predictors, a database including limnological data were assembled for the 49 selected lakes. Measurements for most of the lakes were collected through summer 2013. Missing data were contributed by other sources (table 2). Limnological samples were collected at the deepest point of each lake (Zmax) using pelagic mixed layer samples

from three different depths (top/middle/bottom) in the epilimnion. DOC samples were collected as the filtrate through Whatman GF/F filters and were analysed on an Aurora 1030W TOC Analyser using the persulfate oxidizing reagent method. External standards were included for every sample batch to ensure consistency between each analysis. Color was also measured from this filtrate as absorbance at 440 nm and converted to standard Pt units (mg·l^{-1}) following the Cuthbert and delGiorgio method (1992). TP concentration (ug·l^{-1}) was analyzed by measuring absorbance at 890 nm after persulfate digestion (Wetzel 2001, after Murphy and Riley 1962). pH was measured using a Hanna portable pH meter with an automatic temperature-compensating electrode. Temperature, dissolved oxygen and conductivity profiles were measured using a YSI Pro 2030 meter. Profiles of photosynthetic active radiation (PAR) were measured with an underwater quantum PAR sensor and light meter (LICOR LI-192SA and LICOR LI-250A, LICOR, USA). Secchi depth was also measured over the deepest point of each lake.

Fish data

The Quebec Resource management agency contributed lake trout and walleye data from their fish population surveys. These surveys occurred between 1988 and 2012 across the Quebec province. The assembled database included lake morphology, water quality and individual fish data (i.e. total length, weight, sex, sexual maturity and age from sagittal otoliths and less often, scales). Normalized targeted and random gill-netting methods were used to sample both fish species. The fishing effort was a minimum of 18 hours and covered the period between 6 pm and 9 am in each lake. A minimal fishing effort was also applied in consideration of each lake surface areas to get relative abundance estimates for lake trout populations, *i.e.* catch per unit effort, CPUE (fish·net-night^{-1}) and biomass per unit effort, BPUE (kg fresh weight·net-night^{-1}). Only the fish data from random sampling methods were used to estimate catch relative abundance and biomass. Additionally, data on fish communities allowed the determination of the presence or absence of forage fish species in order to evaluate if lake trout populations were mainly piscivorous or planktivorous. The large range in sample size was partly associated to variation in lake size (*i.e.* 23 to 90 971 ha).

Extensive sampling was not possible without impacting fish populations in smaller lakes which sometimes resulted in smaller sample sizes. We are aware that smaller sample sizes may increase the uncertainty of growth estimates but lakes with highly uncertain estimates have been removed during further lake selection. For detailed sampling methods for walleye and lake trout, refer to SERVICE DE LA FAUNE AQUATIQUE (2011).

Yellow perch data were collected between early May and the end of August 2013. Because of time restrictions, a single survey was executed in each lake. Fish sampling only took place in the littoral area of the lakes, over the thermocline, in order to avoid unnecessary bycatch mortality of non-target fish species. A mix of passive and active sampling gears that consisted of a beach seine (6' high, 25' long, 1/2" mesh size), 10 minnow traps (1" mouth aperture), a fyke net (2" mouth aperture, 4 metal rings, 1/4" mesh size, 2 X 60' long by 5' high wings) and 4 gill nets (4 6,5' high by 25' long pannels/net of 1,5", 2", 2,5" and 3,5" mesh size) were used. For further estimation of population growth, multiple fishing techniques were used in order to get the largest variation in yellow perch size in each lake. Multi-panel gill nets were installed at four randomly determined fishing stations, perpendicular to shore, with small and large meshes alternating from the shore among gill nets. This fishing method was standardized to allow the estimation of CPUE and BPUE. The nets were soaked between 12 and 16 hours overnight, covering the period between 7 pm and 5 am. The deepest part of each gill net was always set above the thermocline or shallower than 8 meters for non-stratified lakes. The same fishing effort was applied to all lakes. All fish species were identified and counted for each panel of each net. The other fishing methods were targeted and thus, capture data from these methods was not used for abundance and biomass estimations. A minimum of 30 yellow perch were selected in order to cover the largest size range to facilitate further measurements of the population growth pattern. Each fish was measured (total length in mm and weight in g) and aged using a thin transverse section (~300 um) of the heaviest sagittal otolith (when both were available). Age determination was based on an unpublished method from John Casselman (Ontario

Ministry of Natural Resource) which was modified by Brian Weidel (United States Geological Survey).

Analysis

We applied the Gallucci and Quinn (1979) parameterization of the von Bertalanffy growth model (VBGM) to individual age-at-length data in order to estimate the early growth rates (*w*) of each fish population. These estimates and their associated confidence intervals were used to compare fish growth between populations for each fish species. This single parameter correspond to the product of the standard von Bertalanffy growth parameters K (instantaneous growth rate) and L_∞ (asymptotic population length) and have greater statistical robustness by accounting for the problem of their intrinsic inverse relationship. Following notes from Charnov (2010), *w* captures some essential features of body-size growth and allows comparison of fish growth at small size and at the size of maximum growth. Thereafter, a lake selection was applied based on the "goodness of the fit" of the VBGM on individual growth data of each fish population as specified by Gallucci and Quinn (1979). Examples of different goodness of fits are shown in figure 2.

The growth estimates were obtained by pooling male and female data for all three species. This was necessary because in many cases, sex-specific data were not available. When dealing with the same problem for lake trout populations, McDermid et *al.* (2010) showed that sexual dimorphism was small compared to among-population variation for various life-history indices and thus, that pooling data across sexes does not prevent detection of inter-population differences.

In addition to DOC, other predictors of fish growth were considered in the analysis in order to isolate the DOC effect. *A-priori* selection of the possible growth predictors involved in fish growth was executed to build the candidate model. The same response variables were used for each species. Total phosphorus (TP) was included as a proxy of lake productivity (Schindler et *al.* 1971; Dillon et Rigler 1974), lake region (referring to its provincial administrative region) to control for region-specific characteristics, latitude to

control for the influence of temperature on fish growth, surface area for the variation in lake size and the estimated population relative abundance (CPUE) to control for the effect of fish abundance on growth. A model selection approach was used to compare multiple competing models representing different combinations of the selected growth predictors, following method described by Johnson and Omland (2004).

Simple linear correlations and weighted multiple regressions (1/ SE) were first used to fit every possible model to observed data using selected predictors. Then, the Akaïke information criterion (AIC) was used as the selection criterion in order to determine the "quality" of the different fitted models. The AICc was chosen instead of AIC because of the bias correction term for small sample sizes. AICc should be used when the number of free parameters, p, exceeds ~ n/40, where n is sample size (Johnson and Omland, 2004). The full AIC-based multi-model inference allowed the identification the single best model and the "best set" of similarly supported models explaining fish growth for each species. We used the automated model selection approach presented by Calgano and Mazancourt (2010) with the *glmulti* function from the {glmulti} package in R (Calgano 2011).

In addition to identifying the best set of models, the model-averaged importance value of each predictor was calculated in order to find which model was better at explaining growth variation for each species. This value corresponds to the sum of the relative evidence weights of all models in which the predictor appears. Model-averaged predictor values are more robust through reducing the model selection bias and accounting for model selection uncertainty (Johnson and Omland, 2004).

Results

Environmental variability

The DOC ranges covered were comparable for yellow perch and walleye (~ 4.0 – 16.0 mg·l^{-1}) but smaller for the 22 lake trout lakes (2.6 – 8.8 mg·l^{-1}). Lakes located in Abitibi represented the majority (75 %) of the darker lakes analysed with DOC concentrations > 8.0 mg·l^{-1} and Secchi depths never exceeding 3 meters. More than 50 % of the lakes with

TP concentrations exceeding 10 ug·l⁻¹ were also situated in Abitibi. Only walleye and yellow perch were sampled in this region simply because lake trout are absent. Because lakes in Abitibi were mainly sampled in order to get walleye data, the cluster of darker lakes in this region can be observed by the stronger correlation (R^2 = 0.84) obtained between DOC and latitude for the 22 walleye lakes (figure 3). Within the 49 lakes analysed, only two were considered hyper-eutrophic with TP concentrations > 100 ug·l⁻¹ and the majority (~ 90 %) were either oligotrophic or mesotrophic with TP concentrations ranging between 4.0 and 30.0 ug·l⁻¹. Surface area was the variable with the largest variation between the 49 lakes, ranging from 29 ha (lake Parker) to more than 90 000 ha (lake Abitibi). The pH did not show much variation between lakes (ranging from 6.5 to 8.6) and thus was not included as a possible growth predictor.

Quality of growth data / estimation of growth rate (w)

The amount and dispersion of fish individual length and age data varied between species and between lakes for each species. This variation can be observed in the estimated growth parameters summary (table 3). In general, walleye data were better suited for estimating the early growth rate (*w*) using the VBGM. Out of 25 walleye lakes with available fish growth and environmental data, 3 were excluded based on the goodness of fit. For lake trout, 17 lakes were excluded out of a total of 39 with available growth and environmental data. Large amount of data were available for walleye and estimates of *w* were generally well constrained, with exception of Gravel lake for which only 20 fish were measured. The amount of data available between lakes was more variable for lake trout than for walleye resulting in larger growth rate confidence intervals. Individual growth data from 30 fish was available for each yellow perch population and 13 lakes were selected out of 18. The low amount of data gave less precise estimations of *w* for this species, resulting in fewer lakes selected and larger confidence intervals for most populations.

Effect of DOC on growth

Early growth rates were strongly negatively correlated to DOC concentration for walleye but not for lake trout or yellow perch. A univariate regression of *w* on DOC showed a significant negative relationship for walleye (P < 0.001, R2 = 0.56) but not for the other two species (figure 4). The negative impact of DOC was fairly strong for walleye; over the range of DOC concentrations (4.6 - 16.0 mg·l^{-1}), we observed a 50 % reduction in early growth rates. Similarly, in the multivariate regression, DOC was the most important predictor of walleye growth. For lake trout and yellow perch, other variables were better predictors for the observed variations in growth (table 4). For all three species, DOC had a negative effect every time it was included in a model.

Growth predictors

The most important predictors of walleye early growth rate were DOC, CPUE, and latitude (respective relative importance: 0.79, 0.60 and 0.35) and the signals of their effect were consistent through the top models summarized in table 4. The best model describing walleye growth included negative effects of DOC and CPUE, and described 58 % of the variability in the early growth rate. Other similarly good models (delta AICc < 2) included DOC alone or combined latitude and CPUE.

None of the predictors were strongly related to lake trout growth rates. TP was the only predictor in the best model and had the highest relative importance of any predictor (0.31). Early growth rates were positively influenced by increasing TP concentration but this predictor alone explained only 6 % of the variability in lake trout early growth rates. Another similarly good model (delta AICc < 2) included the intercept only.

The same pattern was observed for yellow perch, without any strong correlation between DOC and selected predictors. This time, the intercept alone represented the single best model. Latitude was the only predictor in the second best model and explained 12 % of the variability in yellow perch early growth rates. Latitude had the highest relative importance of all predictors (0.26) for yellow perch.

DOC effect on fish relative abundance and biomass

The influence of DOC on fish relative abundance (CPUE) differed between fish species (figure 5). Yellow perch relative abundance was negatively correlated with DOC (P = 0.01, R^2 = 0.48) but no effects were observed for walleye and lake trout. This reduction in yellow perch relative abundance is fairly important; being 50 times lower in the lake with the highest DOC concentration compared to the clearest one. The same negative correlation with DOC at a lesser level was observed for yellow perch BPUE (P=0.01, R^2 = 0.46) and again, no relationship was observed for walleye and lake trout.

Discussion

DOC as a growth predictor

Our results provide only limited support for the hypothesis that DOC controls fish growth in north temperate lakes. Univariate regression revealed a significant negative correlation of walleye *w* and DOC concentration (figure 4). Based on model AICc values from weighted multivariate regressions, DOC also had the highest relative importance for describing walleye growth. Sampled lakes for walleye ranged from 4.3 to 16.0 mg·l^{-1} in DOC, and the reduction in growth seems to appear when DOC concentrations reached approximately 7.0 − 8.0 mg·l^{-1}. Before this threshold, no clear tendency was observed. For yellow perch, even if *w* was not significantly correlated with DOC (P = 0.66), a hump shaped tendency can be observed, with a tipping point situated around the same DOC level as walleye (figure 4). Although the effects of DOC variation could not clearly be assessed for each fish species, it appears that DOC has a general negative impact on fish early growth rates (negative effect every time it was included in a model).

Our results also suggest some evidence that contradicts the hypothesis of DOC-driven variation in growth. While the reduction in walleye early growth rate seemed to be related to an increase in DOC concentration, the effect of regional differences between sampling sites represent an alternative explanation. The majority of high DOC lakes were located in Abitibi, and most of them correspond to lakes sampled for walleye. A large part of this region of the Quebec province is sitting on the clay belt area that is

resulting from glaciolacustrine deposits from the draining of the proglacial Lake Ojibway (Laquerre 2000). The high occurrence of clay soils and wetlands in addition to slow water flowing rate observed in this region results in darker, highly turbid waters (Girard-Cote 2006) and these characteristics allowed us to cover a greater range of DOC concentrations for walleye. However, the higher turbidity created by dissolved clay in Abitibi lakes could be added to the DOC effect on light penetration resulting in an overestimation of the DOC impact. To control for the potential effect of the geographical position of lakes and associated region-specific lake characteristics, the relationship between DOC and walleye growth has been measured separately for Abitibi lakes, and then for all the lakes located outside of the Abitibi region. In both cases, no significant correlations were observed, even with DOC concentrations ranging from 8.08 to 16.04 mg·l^{-1} in Abitibi lakes. This either suggests that other region-specific predictors could be explaining the relationship between DOC and walleye growth or that the negative effect of DOC on growth is happening at lower concentrations than those covered in Abitibi lakes.

Although a slight tendency was observed, there was absence of any strong effect of DOC across the measured gradient for yellow perch (which roughly corresponded to the walleye gradient). However, the uncertainty of yellow perch growth estimates resulting from the small sample size (large confidence intervals, especially at lower DOC concentrations) makes the comparison of yellow perch growth between populations and identification of important growth predictors more difficult. Larger sample sizes would certainly have helped to clarify the observed tendency of decreasing growth and to some extent, the possible existence of a DOC threshold as measured for walleye.

Results for lake trout present ambiguous evidence of the relationship between DOC and fish growth. No DOC effect has been observed in these lakes, suggesting that DOC is not a strong determinant of lake trout growth. The 22 lakes sampled for lake trout are included in the usual light climate range characterizing this species habitat, with DOC

concentration ranging from ~2.6 to 8.8 mg·l^{-1} and Secchi depth ranging from 2.7 to 11.8 meters (Schindler and Gunn 2004). The species is usually associated with the cold and well oxygenated waters of small but deep oligotrophic lakes (Schindler and Gunn 2004). The more specific habitat needs in terms of temperature and oxygen are characteristics that make the lake trout a less generalist species compared to walleye and yellow perch. This is observed when comparing the distribution of the three species through North-America, as the lake trout distribution pattern is less even (see distribution patterns in Bernatchez and Giroux 2012). Considering this species need for clearer, colder and more oxygenated water, it is not surprising that most lakes has low DOC concentrations < 6.5mg·l^{-1}, and only one lake has a relatively high DOC concentration (8.8 mg·l^{-1}). The multiple effects of DOC on lake trout habitat properties have previously been summarized by Schindler and Gunn (2004). Considering its far-reaching effect on chemical, physical and biological aspects of lakes and the higher sensitivity of the species to such changes, DOC could represents a strong determinant of lake trout growth. Although, the range of DOC analysed when testing this question seems to play an important role to determine if such effects could be measured. Observations from Gunn et al. (2001) could explain why no relationships were found the 22 lake trout populations analysed in our study. Water clarity in lake trout lakes is primarily controlled by the concentration of coloured organic matter (Gunn et al. 2004). Based on the comparison of 21 small oligothrophic lake trout lakes with DOC concentration ranging from 0.1 to 4.6 mg·l^{-1}, a reduction of Secchi depth from 27.3 m to ~ 5.7 m was associated with an initial DOC increase from 0.1 to 2.7 mg·l^{-1} (Gunn et al. 2001). This upper limit of DOC concentration (2.7 mg·l^{-1}) corresponded to the lowest in our set of lakes, suggesting that the range where changing DOC concentration have the biggest effect in lake trout habitat was not covered in our lakes. Considering the impact of a variation in lake trout habitat availability on multiple factors influencing the species growth (e.g. temperature, foraging possibilities, resources abundance, energy allocation, etc.), the lack of growth estimations from low DOC lakes is most likely explaining the absence of a relationship here. Additionally, the growth estimates for lake

trout are less precise in comparison to walleye because the growth pattern for this species does not fit as well when using the VBGM.

Species-specific growth predictors

Walleye

Considering that the light attenuation effect of DOC seems to be the main driver through which fish production is lowered in lakes (Karlsson et al. 2009; Craig et al. *in review*), the reduction in light caused by higher DOC concentration is most likely explaining the strong negative influence that has been observed for walleye growth. A model developed by Lester et al. (2004) shows the importance of light, together with temperature and bathymetry in controlling walleye production. Their model proposes an estimation of the benthic area of a lake associated with optimum light and temperature conditions for walleye during an annual cycle (TOHA) as a predictor. When testing the applicability of their model in explaining known walleye yield, they found that little walleye habitat exists in really dark waters. The available TOHA increased rapidly along with initial water clarity increases and then declined exponentially after reaching what corresponds to the optimal water clarity (Lester et al. 2004). These observations agree with the proposition of a DOC threshold separating the positive and negative effects of DOC observed by Finstad et al. (2014), and also propose the same rapid decline in fish production (related here to the TOHA availability) with decreasing water clarity once the optimum is reached. In addition, when considering Abitibi lakes solely, the maximum walleye early growth rates were found in lakes with Secchi depths in order of 2 m (figure 6), which correspond to the optimal water clarity (*i.e.* allows the highest optimal habitat availability) estimated by Lester et al. (2004). A reduction in walleye ability to encounter and capture prey (foraging success) has been proposed to explain the relationship between optimal habitat and production (Lester et al. 2004).

Among factors that have been found to influence walleye production (see reviews by Leach et al. 1977; Kerr 1997 and Holden et al. 2012), water clarity is expected to have important repercussions because it is the main abiotic controlling variable determining

the spatial and temporal dimensions of feeding in walleye (Ryder 1977). The species can tolerate a great range of environmental conditions but mesotrophic lakes with moderate turbidity usually represent optimal conditions (Scott and Crossman, 1973; Kerr 1997). In general, walleye is well adapted to darker, more turbid environment due to the development of a special visual apparatus associated with ontogenetic changes in diet during its first year of life that increase its sensitivity to light (Ryder 1977; Vandenbyllaardt and Ward 1991; Guzevich 1993) and allows adult walleye to feed intermittently through the day (Schlick 1978). A positive effect of moderate turbidity increases are usually observed for planktivorous juvenile walleye that use short distance prey detection, while the opposite effect is observed for adult walleye (Ryder et al. 1977; Giske et al. 1994; Utne-Palm 2002). Accordingly, one can assume that DOC associated growth rates will vary for different fish life stages. Such distinctions were not feasible with the estimation of growth rate based on multiple fish age-classes. Although w in the VBGM represents the rate of fish growth at early life stages, it is also influenced by the growth pattern at later ages (Gallucci and Quinn 1979) and so is a good overall approximation of the fish population growth.

Our results present interesting links to observations made by Lester et al. (2004). However, when measuring the potential effect on fish production in relation to its light attenuation capacity, it is important to assess how DOC concentration is really affecting water clarity by verifying the level of "turbidity" or "darkening" caused by DOC. While multiple factors can reduce light availability in lakes, light scattering (turbidity) and absorption (color) can act independently, resulting in different light attenuation capacities (Koenings and Edmundson 1991). For our lake selection, increasing DOC generally implied a reduction in light availability while being strongly correlated to Secchi depth, color and Kd. (figure 7). The same correlations were observed when only considering the Abitibi lakes but the variation in DOC concentration explained a smaller part of the Secchi depth, suggesting that DOC is not the only driver of water clarity (figure 8). As previously stated, due to the unique geology of this region, both the

amount of clay in suspension and DOC concentration could be controlling the light climate in Abitibi lakes. Lester et al. (2004) also mentioned the implication of the lake basin shape and morphometry in the determination of the walleye optical habitat. This suggests that the optimal DOC concentration allowing a maximal TOHA also varies between lakes, depending on their shape and morphometry. Surface area was the only variable available to control for this.

The relative abundance (CPUE) and latitude had the 2nd and 3rd highest relative importance as predictors for the variation in walleye early growth rate. In addition to their geological particularities, Abitibi lakes are situated at northern latitude. Considering that temperature is arguably one of the most important determinants of walleye growth (Paloheimo and Dickie 1966; Fry 1971; Kitchell et al. 1977; Lester et al. 2004; Venturelli et al. 2010), we considered that the inclusion of latitude as a growth predictor could control for the potential negative effect of a colder climate on walleye growth. When observing the set of best models, one can appreciate the strength of latitude as a growth predictor, as it replaces the DOC effect in the third model.

Even though no correlation was observed in a univariate regression (P = 0.34), CPUE is present in the first and third best models and its negative coefficient could indicate density-dependence of growth in walleye. Density-dependent changes in total body length at age have been observed for many individual walleye populations (Anthony and Jorgensen 1977; Colby and Nepszy 1981; Reid and Momot 1985). Additionally, based on the comparison of multiple walleye populations, Venturelli et al. (2010) observed a twofold difference in immature growth rate caused by the variation in food availability, suggesting a strong density-dependent growth response. Further analysis revealing a 1.3-fold increase in immature walleye growth rate at low abundance vs. high abundance supported this hypothesis (Venturelli et al. 2010).

Yellow perch

None of our models could explain much of the variability in yellow perch growth. Uncertain growth estimates and a limited number of lakes could be partially responsible for this absence of relationships. Precision in growth estimation is essential to measure signals in growth variability; even more so considering that growth is extremely variable between populations for this generalist, widely distributed fish species (Scott and Crossman 1973; Boisclair and Leggett 1989). Several interpretations have been suggested to explain the variability in yellow perch growth, including the presence of a competing species (Boisclair and Leggett 1989; Hayes et al. 1992; Bertolo and Magnan 2005), habitat productivity (Abbey and Mackay 1991), prey type (Tyson and Knight 2001), piscivory (Bertolo and Magnan 2005) and water temperature (Power and van den Heuvel 1999). Our results indicate that, from our available variables, latitude is the most important predictor of early growth rate for yellow perch in our set of lakes (highest relative importance). However, this relationship is weak considering that the intercept is also included in the set of best models and that no correlation is found with univariate regression of w on latitude (P = 0.38). Previous studies have shown a negative effect of colder temperatures (Wang and Eckmann 1994) and higher latitudes (Power and van den Heuvel, 1999) on growth and survival of younger yellow perch. However, it seems that growth reliance on temperature is not as strong for adult yellow perch (Henderson 1985).

Yellow perch populations show a high trophic flexibility but in general, adults are mainly benthivores (Haas and Schaeffer 1992; Vander Zanden and Vadeboncoeur 2002). Important ontogenetic shifts in both diet and habitat are observed for early life stages: a few days after hatching in the littoral zone, young yellow perch move to the pelagic zone to feed on zooplankton and then return to the littoral once they reach a sufficient gape size to integrate benthic prey into their diet (Wang and Eckmann 1994; Post et al. 1990). This ontogenetic shift in diet is accompanied by a change in their vision that is comparable to what is observed for walleye (Whal et al. 1993). By using daily growth estimations for larval and juvenile yellow perch, Leclerc et al. (2011) observed higher

growth rates following an increase in nutrients and DOC concentrations associated with forest harvesting in the catchments of northern Canadian Boreal Shield lakes. It has been proposed that a modification in feeding conditions resulting from a nutrient-driven increase in prey abundance and DOC-driven increase of prey visibility could be explaining this variability in yellow perch growth (Leclerc et al. 2011). However, contrasting observations were made in a similar experiment by St-Onge and Magnan (2000), where no effect of watershed perturbations on yellow perch growth was observed when excluding younger life stages. This suggests that the DOC-growth relationship could differ substantially when including older benthivorous fish. Yellow perch generally prefer clearer water conditions but as with walleye, moderate increases in turbidity are usually beneficial for younger individuals (Giske et al. 1994; Utne-Palm 2002). DOC concentrations measured in lakes analysed by Leclerc et al. (2011) before logging were relatively high (ranging from 7.0 to 9.4 mg·l^{-1}) which makes the positive impact of further increases in DOC on visual prey detection surprising, even for younger planktivorous yellow perch.

Lake trout

As for yellow perch, none of our models explained much of the variability in lake trout growth. The inclusion of more specific growth predictors which are likely to affect lake trout such as diet and temperature/oxygen profiles may have helped explain more of the variability in lake trout growth. The boundaries of lake trout optimal habitat have been defined by temperatures of less than 10 ˚C at the top and by oxygen concentrations greater than 6 mg·l^{-1} at the bottom (Evans et al. 1991). The variation in either nutrient status or transparency of a lake has been shown to have a direct impact on the lake trout optimal habitat volume available by influencing the depth at which these lower and upper boundaries are found (Clark et al. 2004). In general, water clarity in lake trout lakes is controlled by DOC rather than TP and thus, changes in optimal habitat size resulting from a variation in TP would be much less significant than those resulting from DOC-induced modifications in water clarity (Clark et al. 2004). Even though no predictors were strongly related to variation in early growth rates, total

phosphorus had the highest relative importance (0.31). Moreover, a univariate regression of w on TP showed a weak but still significant positive correlation (P = 0.02, R^2 = 0.25). While selected lakes had fairly low TP concentrations (ranging from 2.32 to 16.76 ug·l^{-1}), it seems that this increase is enough to promote lake trout growth. This is possibly explained by the combined positive effect of higher productivity (related to faster juvenile growth and larger maximum sizes for lake trout; McDermid et al. 2010) and increased volume of optimal habitat available. Indeed, while higher nutrient levels can increase oxygen deficits near the bottom of lakes (Molot et al. 1992), the associated increases in chlorophyll a can also result in shallower Secchi depths that raise the upper boundary (Dillon et Rigler 1974). However, as previously mentioned, the inclusion of a lower range of DOC for lake trout could have revealed a stronger DOC-growth relationship.

Lake trout in smaller lakes are more planktivorous and attain smaller body sizes than those in larger lakes (Pazzia et al., 2002). The availability of suitable forage species such as yellow perch, lake whitefish (*Coregonus clupeaformis*) and cisco (*Coregonus artedi*) during the growth season have strong repercussions on lake trout growth efficiency, and the reduction in growth rates of planktivorous lake trout (*e.g.* smaller asymptotic length) have been attributed to a reduction in resource availability (Martin 1952, 1966; McDermid 2007). In general, more complex communities and higher prey abundances are observed in larger lakes (Barbour and Brown 1974). Accordingly, Shuter et al. (1998) suggested that food availability could be explaining the strong relationship between lake trout growth and lake area observed in 54 Ontario lakes. Lake size could also influence the possible impact of DOC-related light attenuation, as the major effects of water clarity on mixing depth and other aspects of thermal stratification are mainly confined to lakes smaller than 500 ha (Fee et al., 1996). Wind and other meteorological events become more important in terms of mixing depths as lake size increases. Considering both the implications of lake size on resource availability and thermal stratification, and that selected lake trout lakes were covering a large range size range (158 - 20 616 ha), the absence of a correlation between surface area and lake trout growth is surprising.

Validating if a change in diet was associated with the variation in lake size would have been helpful but was not possible as diet information for selected populations was either defined as piscivorous or unknown in the supplied datasets.

DOC effect on relative abundance and biomass

Although the estimates of relative abundance and biomass (CPUE/BPUE) were mainly used as a way to control for a possible density-dependence effect in fish growth, they also revealed an important intra-specific variations in yellow perch abundance (mean CPUE: 0.64 ± 0.62, n = 13) along with changes in DOC concentration (figure 5). These results suggest that a reduction of yellow perch production in darker lakes could result from a decrease in yellow perch relative abundance/biomass. Yellow perch abundance was fifty times higher in the lowest-DOC lake when compared to the highest-DOC lake, and again the decrease in abundance seems to happen around ~ 8.0 mg·l^{-1} of DOC. A smaller but still substantial decrease (~ 30 times) has been observed for yellow perch biomass (BPUE) with DOC. For walleye and lake trout, it seems that DOC doesn't have much effect on their relative abundance.

Reductions in yellow perch abundance are usually related to increasing turbidity or decreasing vegetation that respectively affect foraging efficiency and predation risk (Scott and Crossman, 1973). Following observations from Bertolo and Magnan (2005; 2007) both the variation in DOC concentration and the occurrence of piscivorous fish represent potential drivers for the variation in relative abundance of young-of-year (YOY) yellow perch. Higher abundances have been observed following an increase in DOC concentrations caused by perturbations in the lake catchments. To explain this increase in abundance, higher protection against UV radiation and increased secondary production have been proposed (Bertolo and Magnan 2007). A contrasting effect of the occurrence of predator fishes such as northern pike (*Esox lucius*) and walleye was observed on yellow perch abundance, suggesting a strong predation-induced mortality (Bertolo and Magnan 2005). In addition to the direct effect of predation on yellow perch abundance, the use of less-suitable habitat and sub-optimal prey items forced by the

presence of predators in the pelagic habitat could also lead to reduced growth and abundance in yellow perch (Werner et al. 1983). All 13 lakes analysed in our study included at least one species of predator fish (*i.e.* smallmouth bass (*Micropterus dolomeiu*), chain pickerel (*Esox niger*), northern pike, or walleye) which reduced the possibility of a predator-driven variation in abundance between lakes.

The gill nets used for all three species were chosen to ensure the capture of a large size range of fish in order to estimate population growth rate. However, these nets are not efficient in capturing smaller fish. For yellow perch, this selectivity resulted in the exclusion of age 1 and 2 fish in most of the sampled lakes. Considering that the catchability of small size yellow perch could have increased with fish growth as the summer progressed, a possible bias in abundance estimations could be observed if lakes where lower abundances were measured were systematically sampled early in the summer (St-Onge and Magnan 2000) which was not the case for our set of lakes.

The variation in relative abundance and biomass estimates for lake trout populations are respectively 12 and 26 times higher than the variation in early growth rates, which should be enough to reveal a relationship with changing DOC, if any. While no relationship with DOC concentration was observed, both relative abundance and biomass were correlated with TP (P < 0.05, R^2 = 0.26 and 0.36 respectively) and latitude (P = 0.01, R^2 = 0.38 and P = 0.01, R^2 = 0.48 respectively). The higher importance given to TP concentration for lake trout reflects a nutrient limitation of production for this species, and gives less credit to a possible relationship with DOC. This is in contradiction to previous results relating a negative (Karlsson et al. 2009) or unimodal (Finstad et al. 2014) correlation between DOC and biomass for other salmonid species (arctic char - *Salvelinus alpines* and brown trout, *Salmo trutta*). The reduction in fish production in darker waters observed by Karlsson et al. (2009) included estimates from Eurasian perch (*Perca fluviatilis*) populations. The greater similarity between arctic char and lake trout could result in a more similar response to changes in lake characteristics but the Eurasian perch represent contrasting morphology, physiology and ecology that relates

strongly to yellow perch (Rougeot et al. 2002). While Karlsson et al. (2009) paper does not mention the respective contribution of each species in this observed relationship with light attenuation; the outcome may be different if considering them separately.

The smaller intra-specific variation in abundance for walleye suggests that the changes in relative abundance were possibly too low to be associated to any of the predictors. However, this variation was important enough to suggest a density-dependence of walleye growth in selected walleye lakes. Previous observations made by Lester et al. (2004) suggesting a strong relationship between walleye production and factors that influence their ability to encounter and capture prey (*i.e.* light, temperature and lake bathymetry) did not make a clear distinction between the respective contribution of growth and abundance to production. This suggests that the same drivers that influence walleye growth could possibly explain changes in the species abundance. Even if DOC was not correlated with CPUE or BPUE, a tendency of decreasing abundance and biomass with increasing DOC could still be observed.

Our results provides only limited support that indices of fish production are negatively correlated with DOC concentrations in temperate lakes, as proposed by recent observations from Karlsson et al., (2009) and Finstad et al. (2014). In general, the patterns of variation in growth and relative abundance for yellow perch and walleye suggested a negative effect of higher DOC concentrations. For both species, production could be positively affected by initial increases in DOC until reaching an "optimal" DOC concentration. Further increases in DOC would then have the opposite effect on fish production. The existence of this hypothetical threshold is partly supported by previous observations suggesting that a certain DOC concentration needs to be reached before a reduction in secondary production could be observed (Kelly et al. 2014; Craig et al. *in review*). The relationship between walleye production and habitat characteristics (light, temperature, basin shape and morphometry) proposed by Lester et al. (2004) also suggests a possible unimodal relationship between light levels and production. This unimodal relationship was also described by Finstad et al. (2014) for brown trout.

However, we need to be careful with this proposition, considering that the same DOC concentrations can have a very different impact in lakes depending on variations in their shape and morphometry. Even if a moderate concentration of DOC is preferable for percids (Utne-Palm 2002; Lester et al. 2004), the possible positive effect of the initial increase in DOC could not be analysed in this study due to a lack of lakes with lower DOC concentrations. In addition, observations for yellow perch are less likely to be a good representation of the DOC-production dynamic for this species considering the uncertainty of our production estimates. For lake trout, our results suggest that lake productivity (estimated by TP), not DOC, is the main driver of changes in both growth and relative abundance. However, we suppose that a negative effect of DOC would have been observed if lakes with lower DOC concentration were included.

Based on results from Vander Zanden and Vadeboncoeur (2002), all three fish species included in our study rely strongly on zoobenthos as a resource, determined either by direct consumption of zoobenthic prey, or indirectly through consumption of prey fish feed on zoobenthos. For piscivorous species (pike, walleye and lake trout), reliance on zoobenthos averaged 64 %, from which more than 35 % represented indirect reliance. In addition, around 50 % of prey fish consumed by both walleye and lake trout were supported by zoobenthos (Vander Zanden and Vadeboncoeur 2002). Considering the proposition that a reduction in zoobenthic prey availability associated with increases in DOC could explain the reduction in fish production (Craig et al. *in review*), and that reliance of zoobenthos is widely variable for different fish species (Vander Zanden and Vadeboncoeur 2002), the assumption of a DOC species-specific effect is highly plausible. However, evaluating to what extent the intra-specific variation in production is related to changes in DOC concentration could be harder considering that reliance on zoobenthic prey also variable among populations of a given species (Vander Zanden and Vadeboncoeur 2002). We think that the use of early growth rate estimates, even if simplistic, represents a good way to verify larger patterns in growth of fish populations. Based on our findings, we suggest that both a reduction in fish growth and/or abundance in high DOC lakes could contribute to lower fish production in north

temperate lakes, and that the importance of a DOC-driven effect on fish production is most likely to vary for different fish species. Higher reliance of walleye and yellow perch on zoobenthic prey in comparison to lake trout (Vander Zanden and Vadeboncoeur 2002) makes the relationship between DOC and zoobenthos production described by Craig et al. (*in review*) more likely to explain observed changes in production for all three species.

Conclusion

The central role of DOC as a fundamental variable in controlling freshwater ecosystems structure and function and production at higher trophic levels is now well recognised. However, there are still many gaps to be filled in order to get a better understanding of the possible consequences of the ongoing increases in DOC on fish population production and the underlying mechanisms. Our results confirm that DOC concentrations have a negative species-specific impact on fish early growth rates and abundance, and thus, on fish production. Considering the light attenuation effect of DOC, this negative impact could possibly be related to an effect on light, temperature, and oxygen distribution in the water column, with concomitant impacts on fish habitat, foraging efficiency and resource availability. We proposed that a reduction in zoobenthic prey availability could probably explain the negative effect of DOC that appeared for walleye and yellow perch but production at lower trophic levels could not be measure and accounted for in this study. The negative relation between DOC and growth for important recreational fish species like walleye could have important socio-economic consequences. Even though understanding the global effect of DOC on fish production is essential, the relationships observed in this study revealed the importance of appreciating how the potential impacts of DOC could differ for species depending on their biology, behavior, and life-history.

While surveys across space represent a good way to get information on the global influence of DOC concentrations on fish production, the determination of the main growth predictors is challenging because of high heterogeneity between lakes and

interdependence between predictors. Expanding our dataset by including more lakes and a bigger sample size for each species would allow us to get more precise growth estimates, and a better evaluation the main growth predictors. This might be feasible for species that are of higher importance for management agencies. More precise measurement of species-specific growth predictors and production estimates for lower trophic levels would also have been highly beneficial in order to better control for the variability in growth due to other environmental factors. While DOC concentrations covered for each species were a good representation of the gradient usually observed in north temperate lakes, more growth data on populations evolving in clearer conditions would be useful to get a better understanding of the relationship between the initial increases in DOC and fish growth.

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Table 1. Selected physico-chemical and morphometric predictors of 49 sampled lakes, and their minimum, maximum, mean and standard deviation values.

Lake	Region	Lat	Long	pH	TP (ugl^{-1})	DOC (mgl-1)	Surface area (ha)	Max depth (m)	Secchi (m)	Kd (m^{-1})
Abitibi	Abitibi (8)	48,69	-79,71	8,0	159,54	16,04	90971	15,0	0,29	6,07
Saint-François, Petit lac	Estrie (5)	45,54	-72,04	8,1	146,65	7,42	79	2,5	0,39	3,72
Malartic	Abitibi (8)	48,27	-78,10	7,2	54,60	14,51	7640	17,0	0,48	4,55
Bécancour	Chaudière-Appalaches (12)	46,07	-71,24	7,6	23,09	15,75	97	2,2	0,89	3,35
Duparquet	Abitibi (8)	48,48	-79,27	7,6	38,01	14,09	4558	11,0	0,89	3,14
Louise	Estrie (5)	45,73	-71,42	7,7	22,04	9,47	398	9,2	0,98	2,04
Témiscamingue	Abitibi (8)	47,40	-79,53	-	15,14	8,08	29485	213,0	1,24	-
Beauchastel	Abitibi (8)	48,15	-79,10	8,5	23,33	11,09	868	31,0	1,36	2,03
Guéguen	Abitibi (8)	48,10	-77,22	7,0	14,15	10,41	5154	13,0	1,53	2,46
Preissac	Abitibi (8)	48,33	-78,35	7,2	19,93	11,85	7252	16,0	1,55	2,01
D'Alembert	Abitibi (8)	48,38	-79,01	7,4	16,74	12,28	109	7,0	1,66	2,24
Aylmer	Estrie (5)	45,84	-71,34	7,2	12,77	9,69	3331	36,0	1,84	1,90
Parker	Estrie (5)	45,33	-72,31	7,6	12,39	6,74	23	8,5	1,90	1,29
Dasserat	Abitibi (8)	48,25	-79,41	8,0	14,09	10,81	2823	17,0	1,91	1,87
Saint-François, Grand lac	Chaudière-Appalaches (12)	45,92	-71,15	7,5	12,77	10,00	5120	40,0	1,92	1,93
Joannès	Abitibi (8)	48,19	-78,68	7,4	8,10	14,55	430	30,0	1,97	2,43
Opasatica	Abitibi (8)	48,08	-79,31	8,4	12,32	9,58	5128	60,0	2,20	2,16
Labyrinthe	Abitibi (8)	48,24	-79,50	8,0	11,78	11,36	787	11,0	2,33	1,84
Blanchin	Abitibi (8)	48,10	-77,06	7,0	8,17	8,64	264	7,0	2,42	1,91
Argile, de l'	Outaouais (7)	45,86	-75,56	8,6	15,38	5,09	451	43,0	2,68	0,75
Vaudray	Abitibi (8)	48,09	-78,68	7,0	6,75	11,59	746	33,0	2,68	1,94
Huit, Lac du	Chaudière-Appalaches (12)	46,08	-71,20	7,4	13,10	8,77	240	19,5	2,78	1,73
Pohénégamook	Bas-Saint-Laurent (1)	47,49	-69,27	-	4,84	6,45	894	41,0	2,81	-
Tapani	Laurentides (15)	46,91	-75,33	7,8	8,83	6,90	653	42,0	2,92	1,06
Matchi-Manitou	Abitibi (8)	48,01	-77,05	7,1	5,39	8,79	3781	65,0	2,97	1,61
Magog	Estrie (5)	45,30	-72,04	8,4	8,59	4,11	1150	19,0	3,49	0,64
Massawippi	Estrie (5)	45,21	-72,00	8,5	9,26	3,96	1792	86,0	3,73	-
Nominingue	Laurentides (15)	46,43	-74,98	7,3	6,19	4,32	2211	36,4	3,79	-
Saint-Paul	Laurentides (15)	46,71	-75,33	8,0	7,14	6,53	515	32,8	3,83	0,83
Brompton	Estrie (5)	45,42	-72,15	7,4	8,35	5,89	1191	42,4	4,00	-
Saint-Joseph	Capitale-Nationale (3)	46,91	-71,64	6,9	5,50	2,99	1118	37,0	4,16	-
Chibougamau	Nord-du-Québec (10)	49,84	-74,23	7,9	4,24	5,31	20616	59,0	4,20	-
Nominingue, Petit lac	Laurentides (15)	46,37	-75,02	-	5,53	5,01	653	38,5	4,26	-
Matapédia	Bas-Saint-Laurent (1)	48,55	-67,56	-	4,19	4,54	3807	42,0	4,46	-
Poisson Blanc	Outaouais (7)	45,97	-75,74	8,0	9,32	4,77	5282	124,0	4,59	0,81
Blue Sea	Outaouais (7)	46,22	-76,05	8,4	5,59	3,91	1437	60,0	4,73	0,36
Gravel	Laurentides (15)	46,80	-75,38	7,7	6,93	5,26	166	34,0	4,85	0,89
Jerry	Bas-Saint-Laurent (1)	47,43	-68,79	-	4,02	3,40	588	48,0	5,00	-
Témiscouata	Bas-Saint-Laurent (1)	47,75	-68,89	-	4,62	5,32	6682	75,0	5,09	-
Sables, Lac aux	Mauricie (4)	46,88	-72,36	6,5	2,32	3,38	531	41,0	5,31	-
Cèdres, Grand lac des	Outaouais (7)	46,30	-76,11	8,3	7,07	4,30	793	39,0	5,64	0,44
Simon	Outaouais (7)	45,97	-75,08	7,3	3,62	4,28	2849	109,0	5,81	-
Louisa	Laurentides (15)	45,77	-74,42	7,5	3,85	3,75	442	56,6	6,05	-
Tremblant	Laurentides (15)	46,25	-74,64	-	2,11	3,41	967	97,4	6,25	-
Cerf, Grand lac du	Laurentides (15)	46,28	-75,50	-	3,46	3,79	1267	120,0	6,59	-
31 Milles, Des	Outaouais (7)	46,19	-75,81	8,3	6,09	4,03	4973	88,0	7,50	0,40
Memphrémagog	Estrie (5)	45,03	-72,24	8,3	16,76	2,86	9531	107,0	8,15	0,51
Viceroy	Outaouais (7)	45,85	-75,11	-	4,70	2,57	158	37,0	8,97	-
Vert	Outaouais (7)	46,00	-75,80	8,4	4,40	3,72	179	44,0	11,80	0,26
	Minimum			6,5	2,11	2,57	23	2,20	0,29	0,26
	Maximum			8,6	159,54	16,04	90971	213,00	11,80	6,07
	Mean			7,7	16,81	7,38	4902	46,18	3,61	1,85
	Standard deviation			0,5	29,92	3,82	13594	39,45	2,39	1,28

Table 2. Complementary data sources for physico-chemical, morphometric and biological variables.

Data	Sources
Lake trout/walleye capture and individual growth.	• Ministère des Ressources Naturelles et de la Faune (MRNF)
Water-chemistry and morphometry	• Metadatabase from Beatrix Beisner - UQAM • Metadatabase from Carbon Biogeochemistry of Boreal Awuatic Systems (CarBBAS) - UQAM • Metadatabase from Paul delGiorgio - UQAM • Ministère des Ressources Naturelles et de la Faune (MRNF) • Ministère du Développement durable, de l'Environnement, de la Faune et des Parcs (MDDEFP), 2014. Banque de données sur la qualité du milieu aquatique (BQMA), Québec, Direction du suivi de l'état de l'environnement.

*UQAM: Université du Québec à Montréal.

Table 3. Summary of estimated growth parameters for sampled walleye, lake trout and yellow perch populations. Fish relative abundance was estimated from "catch per unit of effort" data (CPUE).

Lake	Region	Lat	Long	walleye					yellow perch					lake trout					Diet
				N	w	k	t0	CPUE	N	w	k	t0	CPUE	N	w	k	t0	CPUE	
Abitibi	Abitibi (8)	48,69	-79,71	402	66,93	0,10	-2,59	5,19	-	-	-	-	-	-	-	-	-	-	-
Saint-François, Petit lac	Estrie (5)	45,54	-72,04	-	-	-	-	-	60	61,26	0,18	-0,34	1,16	-	-	-	-	-	-
Malartic	Abitibi (8)	48,27	-78,10	745	83,52	0,21	-2,22	10,12	-	-	-	-	-	-	-	-	-	-	-
Bécancour	Chaudière-Appalaches (12)	46,07	-71,24	-	-	-	-	-	57	46,62	0,11	-0,36	0,25	-	-	-	-	-	-
Duparquet	Abitibi (8)	48,48	-79,27	979	52,06	0,08	-3,83	12,39	-	-	-	-	-	-	-	-	-	-	-
Louise	Estrie (5)	45,73	-71,42	-	-	-	-	-	46	82,68	0,27	-0,01	0,28	-	-	-	-	-	-
Témiscamingue	Abitibi (8)	47,40	-79,53	579	75,07	0,14	-2,29	16,78	-	-	-	-	-	-	-	-	-	-	-
Beauchastel	Abitibi (8)	48,15	-79,10	205	51,38	0,05	-1,66	34,17	-	-	-	-	-	-	-	-	-	-	-
Guéguen	Abitibi (8)	48,10	-77,22	369	77,97	0,12	-2,01	12,33	-	-	-	-	-	-	-	-	-	-	-
Preissac	Abitibi (8)	48,33	-78,35	1728	67,03	0,09	-2,05	17,75	-	-	-	-	-	-	-	-	-	-	-
D'Alembert	Abitibi (8)	48,38	-79,01	235	77,13	0,12	-2,01	47,00	-	-	-	-	-	-	-	-	-	-	-
Aylmer	Estrie (5)	45,84	-71,34	120	119,17	0,23	-1,57	4,08	43	93,10	0,29	-0,01	0,08	-	-	-	-	-	-
Parker	Estrie (5)	45,33	-72,31	-	-	-	-	-	68	87,65	0,38	-0,08	1,38	-	-	-	-	-	-
Dasserat	Abitibi (8)	48,25	-79,41	1171	90,17	0,12	-1,66	18,01	59	69,52	0,27	-0,59	0,19	-	-	-	-	-	-
Saint-François, Grand lac	Chaudière-Appalaches (12)	45,92	-71,15	-	-	-	-	-	62	55,67	0,18	-0,74	0,85	-	-	-	-	-	-
Joannès	Abitibi (8)	48,19	-78,68	77	89,48	0,12	-1,71	5,22	66	50,72	0,12	-0,71	0,20	-	-	-	-	-	-
Opasatica	Abitibi (8)	48,08	-79,31	969	90,96	0,15	-1,63	13,37	58	51,64	0,17	-0,71	0,32	-	-	-	-	-	-
Labyrinthe	Abitibi (8)	48,24	-79,50	458	77,71	0,10	-1,74	17,10	-	-	-	-	-	-	-	-	-	-	-
Blanchin	Abitibi (8)	48,10	-77,06	101	106,30	0,20	-1,78	8,42	-	-	-	-	-	-	-	-	-	-	-
Argile, de l'	Outaouais (7)	45,86	-75,56	-	-	-	-	-	-	-	-	-	-	484	110,89	0,17	-0,36	10,85	Ichtyo
Vaudray	Abitibi (8)	48,09	-78,68	151	76,83	0,10	-1,33	21,57	71	60,87	0,18	-0,64	0,04	-	-	-	-	-	-
Huit, Lac du	Chaudière-Appalaches (12)	46,08	-71,20	-	-	-	-	-	47	160,10	0,56	0,48	0,80	-	-	-	-	-	-
Pohénégamook	Bas-Saint-Laurent (1)	47,49	-69,27	-	-	-	-	-	-	-	-	-	-	34	143,37	0,19	0,47	-	-
Tapani	Laurentides (15)	46,91	-75,33	212	176,81	0,26	-0,95	-	-	-	-	-	-	-	-	-	-	-	-
Matchi-Manitou	Abitibi (8)	48,01	-77,05	257	72,43	0,11	-1,99	6,76	-	-	-	-	-	46	90,78	0,09	1,22	0,61	Ichtyo
Magog	Estrie (5)	45,30	-72,04	-	-	-	-	-	64	49,97	0,14	-0,78	2,16	-	-	-	-	-	-
Massawippi	Estrie (5)	45,21	-72,00	-	-	-	-	-	-	-	-	-	-	818	76,00	0,08	-1,41	8,99	-
Nominingue	Laurentides (15)	46,43	-74,98	694	150,01	0,25	-1,34	16,28	-	-	-	-	-	52	139,98	0,18	-1,05	1,70	-
Saint-Paul	Laurentides (15)	46,71	-75,33	-	-	-	-	-	75	64,03	0,20	-0,39	0,64	-	-	-	-	-	-
Brompton	Estrie (5)	45,42	-72,15	-	-	-	-	-	-	-	-	-	-	42	126,37	0,20	-0,29	15,00	-
Saint-Joseph	Capitale-Nationale (3)	46,91	-71,64	-	-	-	-	-	-	-	-	-	-	69	112,91	0,17	2,58	-	-
Chibougamau	Nord-du-Québec (10)	49,84	-74,23	732	114,41	0,17	-0,82	-	-	-	-	-	-	100	87,15	0,11	-2,93	-	-
Nominingue, Petit lac	Laurentides (15)	46,37	-75,02	72	98,32	0,16	-1,61	-	-	-	-	-	-	-	-	-	-	-	-
Matapédia	Bas-Saint-Laurent (1)	48,55	-67,56	-	-	-	-	-	-	-	-	-	-	490	87,31	0,09	-1,33	-	-
Poisson Blanc	Outaouais (7)	45,97	-75,74	219	176,35	0,31	-1,26	12,86	-	-	-	-	-	-	-	-	-	-	Ichtyo
Blue Sea	Outaouais (7)	46,22	-76,05	-	-	-	-	-	-	-	-	-	-	337	131,48	0,16	0,03	7,60	Ichtyo
Gravel	Laurentides (15)	46,80	-75,38	20	144,38	0,22	-1,49	-	-	-	-	-	-	-	-	-	-	-	-
Jerry	Bas-Saint-Laurent (1)	47,43	-68,79	-	-	-	-	-	-	-	-	-	-	108	100,32	0,13	-0,61	4,70	-
Témiscouata	Bas-Saint-Laurent (1)	47,75	-68,89	-	-	-	-	-	-	-	-	-	-	567	120,87	0,14	-0,14	0,19	-
Sables, Lac aux	Mauricie (4)	46,88	-72,36	-	-	-	-	-	-	-	-	-	-	45	83,96	0,11	-0,39	0,70	-
Cèdres, Grand lac des	Outaouais (7)	46,30	-76,11	-	-	-	-	-	-	-	-	-	-	38	119,41	0,15	0,35	2,17	Ichtyo
Simon	Outaouais (7)	45,97	-75,08	-	-	-	-	-	-	-	-	-	-	503	98,43	0,15	-0,09	4,07	Ichtyo
Louisa	Laurentides (15)	45,77	-74,42	-	-	-	-	-	-	-	-	-	-	53	76,08	0,08	-2,13	-	-
Tremblant	Laurentides (15)	46,25	-74,64	-	-	-	-	-	-	-	-	-	-	141	84,07	0,08	-1,23	-	-
Cerf, Grand lac du	Laurentides (15)	46,28	-75,50	-	-	-	-	-	-	-	-	-	-	38	113,54	0,18	-1,42	2,74	-
31 Milles, Des	Outaouais (7)	46,19	-75,81	-	-	-	-	-	-	-	-	-	-	765	96,39	0,12	-0,27	3,30	Ichtyo
Memphrémagog	Estrie (5)	45,03	-72,24	-	-	-	-	-	-	-	-	-	-	786	212,15	0,27	0,77	5,29	Ichtyo
Viceroy	Outaouais (7)	45,85	-75,11	-	-	-	-	-	-	-	-	-	-	36	157,49	0,20	0,17	2,44	Ichtyo
Vert	Outaouais (7)	46,00	-75,80	-	-	-	-	-	-	-	-	-	-	54	73,52	0,12	-0,92	4,13	Ichtyo
	Minimum			20	51,38	0,05	-3,83	4,08	43	46,62	0,11	-0,78	0,04	34	73,52	0,08	-2,93	0,19	-
	Maximum			1728	176,81	0,31	-0,82	47,00	75	160,10	0,56	0,48	2,16	818	212,15	0,27	2,58	15,00	-
	Mean			477	97,02	0,15	-1,80	15,52	60	71,83	0,23	-0,37	0,64	255	111,02	0,14	-0,41	4,65	-
	Standard deviation			435	36,15	0,07	0,62	10,63	10	30,47	0,13	0,38	0,62	282	32,69	0,05	1,17	4,09	-

*CPUE units: Walleye and lake trout = fish·net-night^{-1}, yellow perch = fish·net-hours^{-1}.

Table 4. For the 8 first candidate models explaining variation in fish growth for each species, estimates of the parameters, Δ in AICc scores, Akaike weight, R^2 and the relative importance of each predictor. The models are sorted from best to worst. In order: walleye, lake trout and yellow perch.

Model	TP	Lat	DOC	SA	CPUE	Region	Δ_{AICc}	Akaike weight	R^2
Walleye									
1	-	-	-0.69	-	-0.11	-	0.00	0.26	0.58
2	-	-	-0.64	-	-	-	0.55	0.19	0.58
3	-	-0.32	-	-	-0.07	-	1.62	0.11	0.54
4	-	-0.05	-0.61	-	-	-	2.57	0.07	0.59
5	-	-0.12	-0.47	-	-0.10	-	3.29	0.05	0.59
6	-	-	-0.64	-1.99e-07	-	-	3.56	0.04	0.58
7	-0.006	-	-0.63	-	-	-	3.56	0.04	0.58
8	-	-	-0.67	-1.37e-06	-0.14	-	3.58	0.04	0.58
Relative importance	0.18	0.35	0.79	0.15	0.60	0.01			
Lake trout									
1	-	-	-	-	-	-	0.00	0.31	-
2	0.12	-	-	-	-	-	1.26	0.17	0.06
3	-	-0.01	-	-	-	-	2.64	0.08	0.003
4	-	-	-0.02	-	-	-	2.70	0.08	2.52e-04
5	-	-	-	-6.98e-07	-	-	2.70	0.08	1.50e-04
6	-	-	-	-	-0.02	-	4.01	0.04	0.01
7	0.13	-	-0.06	-	-	-	4.19	0.04	0.07
8	0.13	0.01	-	-	-	-	4.21	0.04	0.07
Relative importance	0.31	0.19	0.19	0.18	0.08	<0.001			
Yellow perch									
1	-	-	-	-	-	-	0.00	0.36	-
2	-	-0.10	-	-	-	-	1.57	0.17	0.14
3	-	-	-0.28	-	-	-	2.42	0.11	0.08
4	-	-	-	-1.85e-05	-	-	3.30	0.07	0.01
5	0.03	-	-	-	-	-	3.39	0.07	0.006
6	-	-	-	-	0.02	-	3.43	0.07	0.003
7	-	-0.12	-	-	-0.06	-	5.46	0.02	0.17
8	-0.06	-0.11	-	-	-	-	5.69	0.02	0.15
Relative importance	0.12	0.26	0.18	0.13	0.13	0.002			

Fig. 1 Lakes location in the southern part of the Quebec Province, showing their wide repartition from East to West.
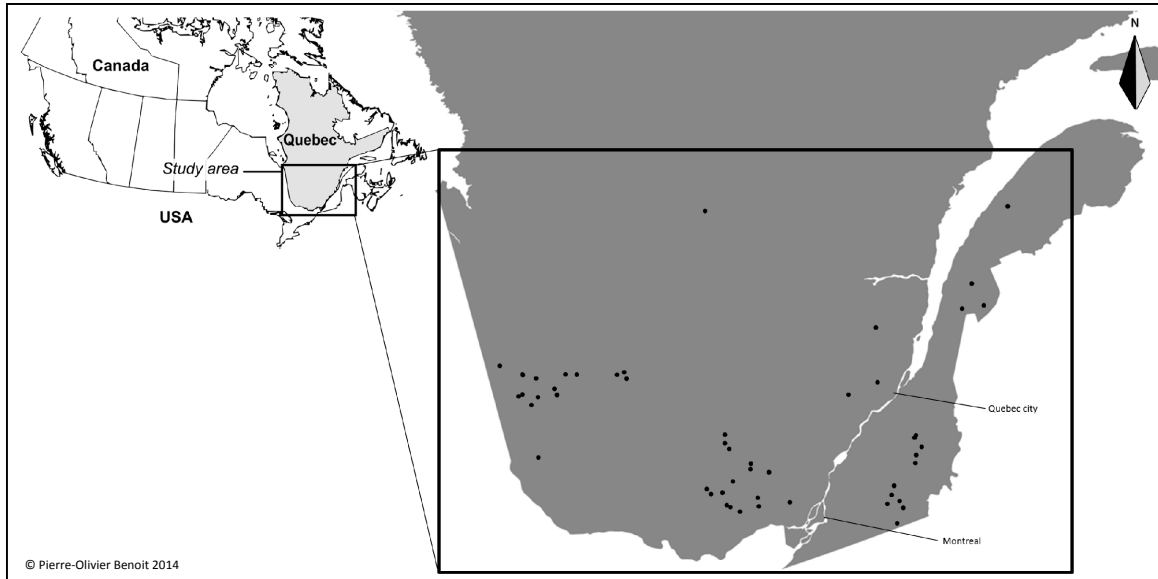
Fig. 2 Comparison of two different lake trout lakes where the von Bertalanffy growth model is presenting a bad (A) and a good (B) fit of individual length-at-age data.
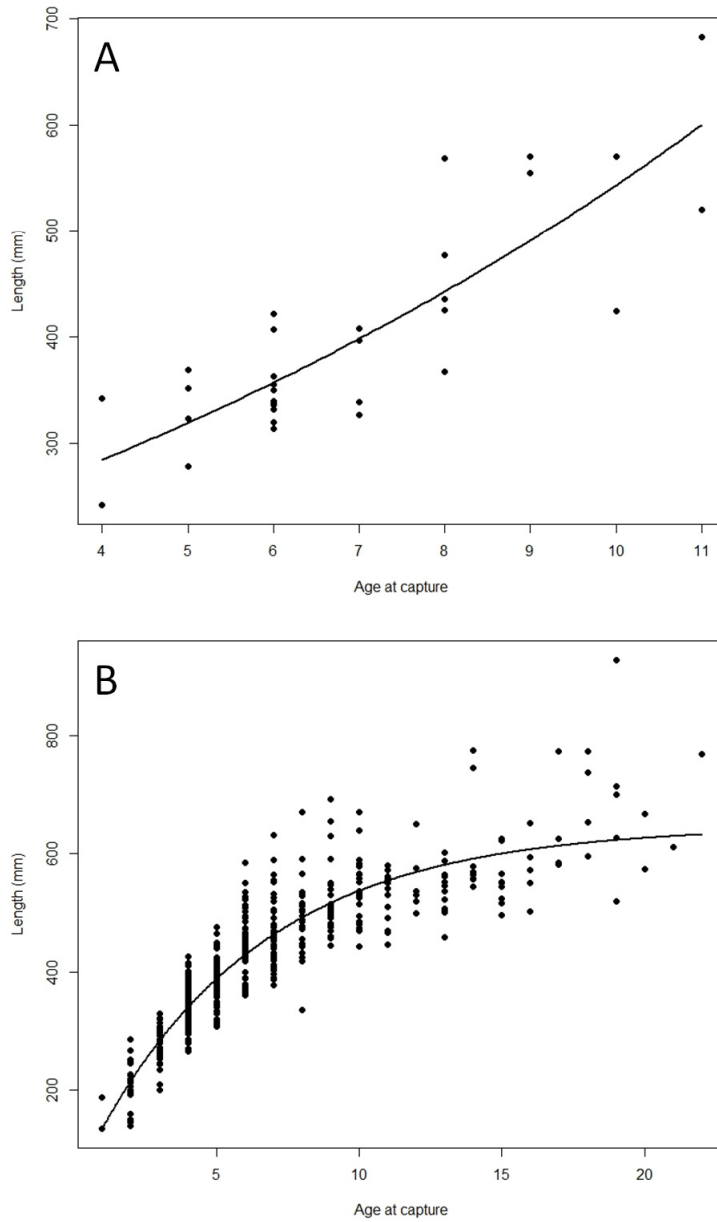
Fig. 3 Relation between DOC and latitude for the 49 selected lakes. Color code: blue = lake trout, red = walleye, black = yellow perch.

Fig. 4 Relation between population early growth rate – w and DOC concentration for each fish species. Confidence intervals are shown for each lakes.
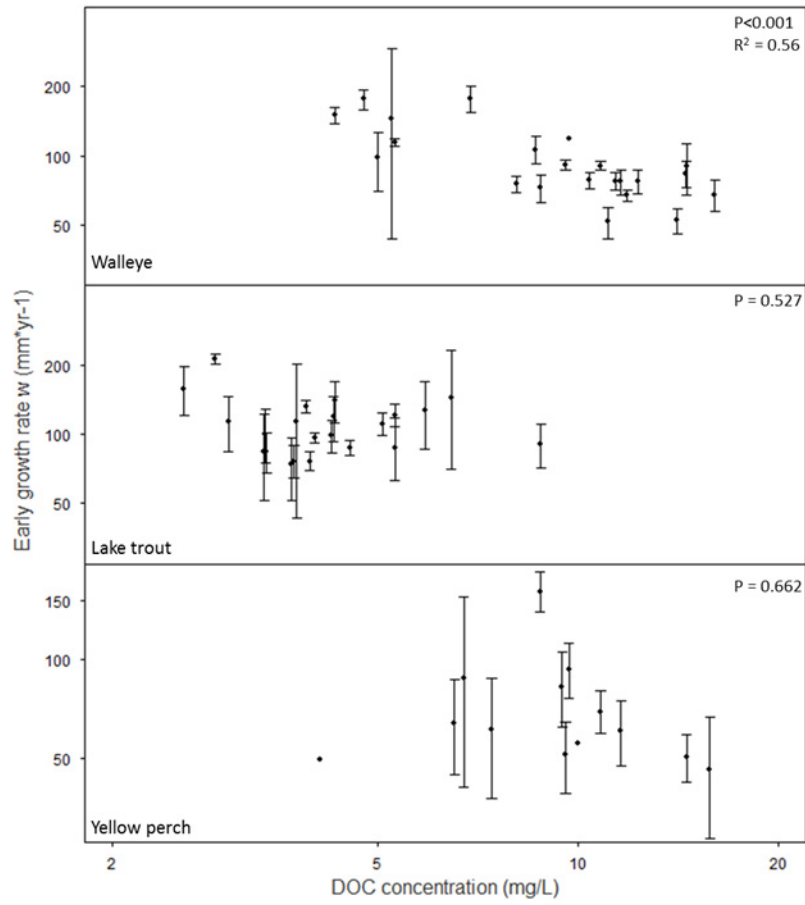
Fig. 5 Relation between fish relative abundance estimates (CPUE) and DOC concentration for each fish species. CPUE units: Walleye and lake trout = fish·net-night^{-1}, yellow perch = fish·net-hours^{-1}.
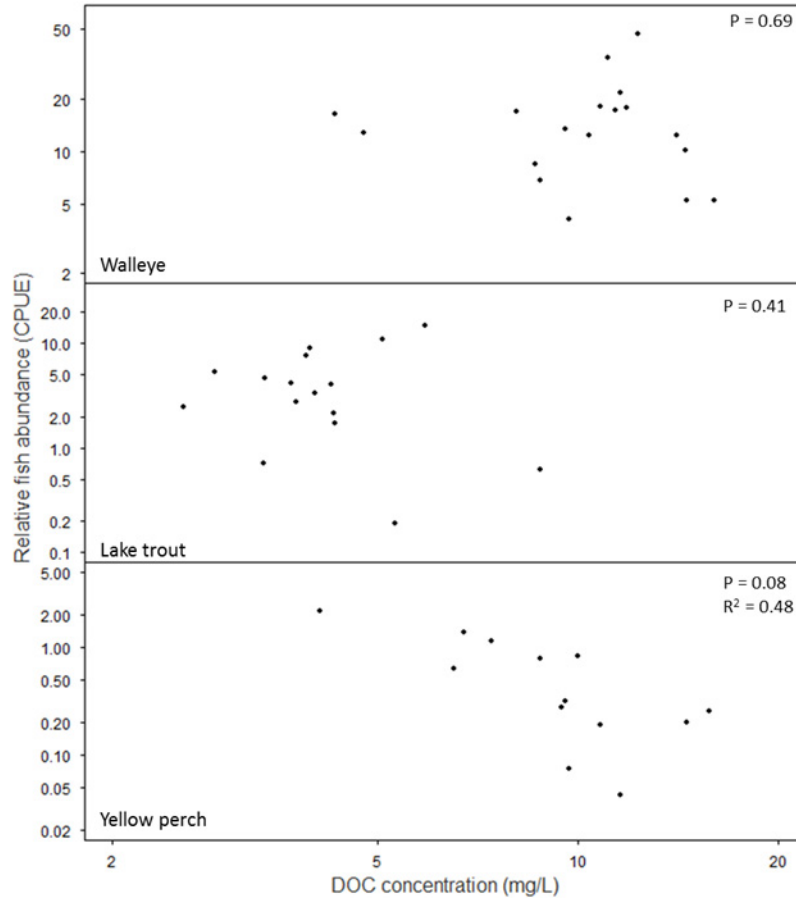
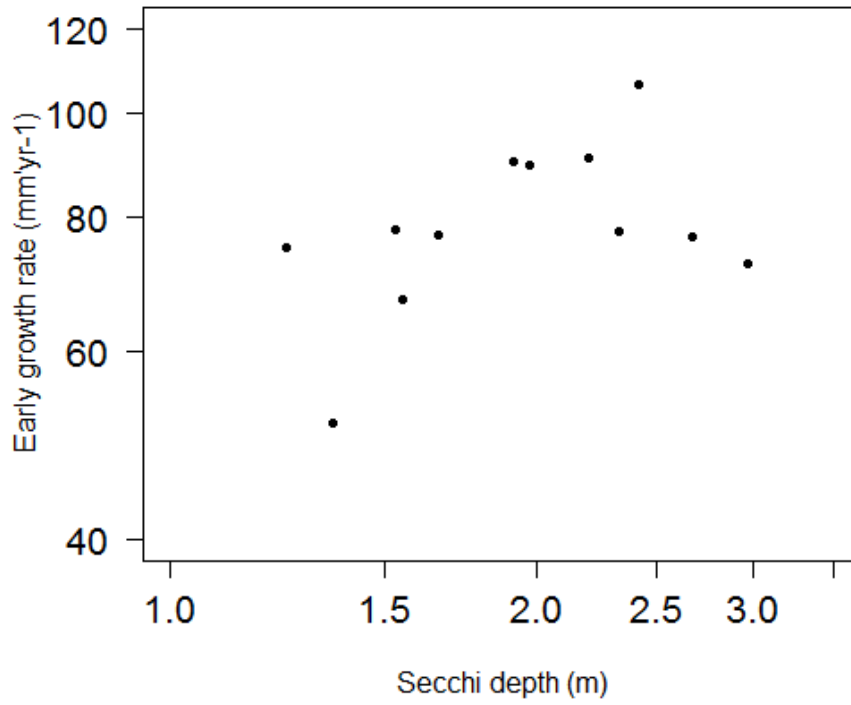Fig. 6 Walleye early growth rate variation with Secchi depth in 12 Abitibi lakes.

Fig. 7 Correlations between water clarity related measurements for all 49 sampled lakes.
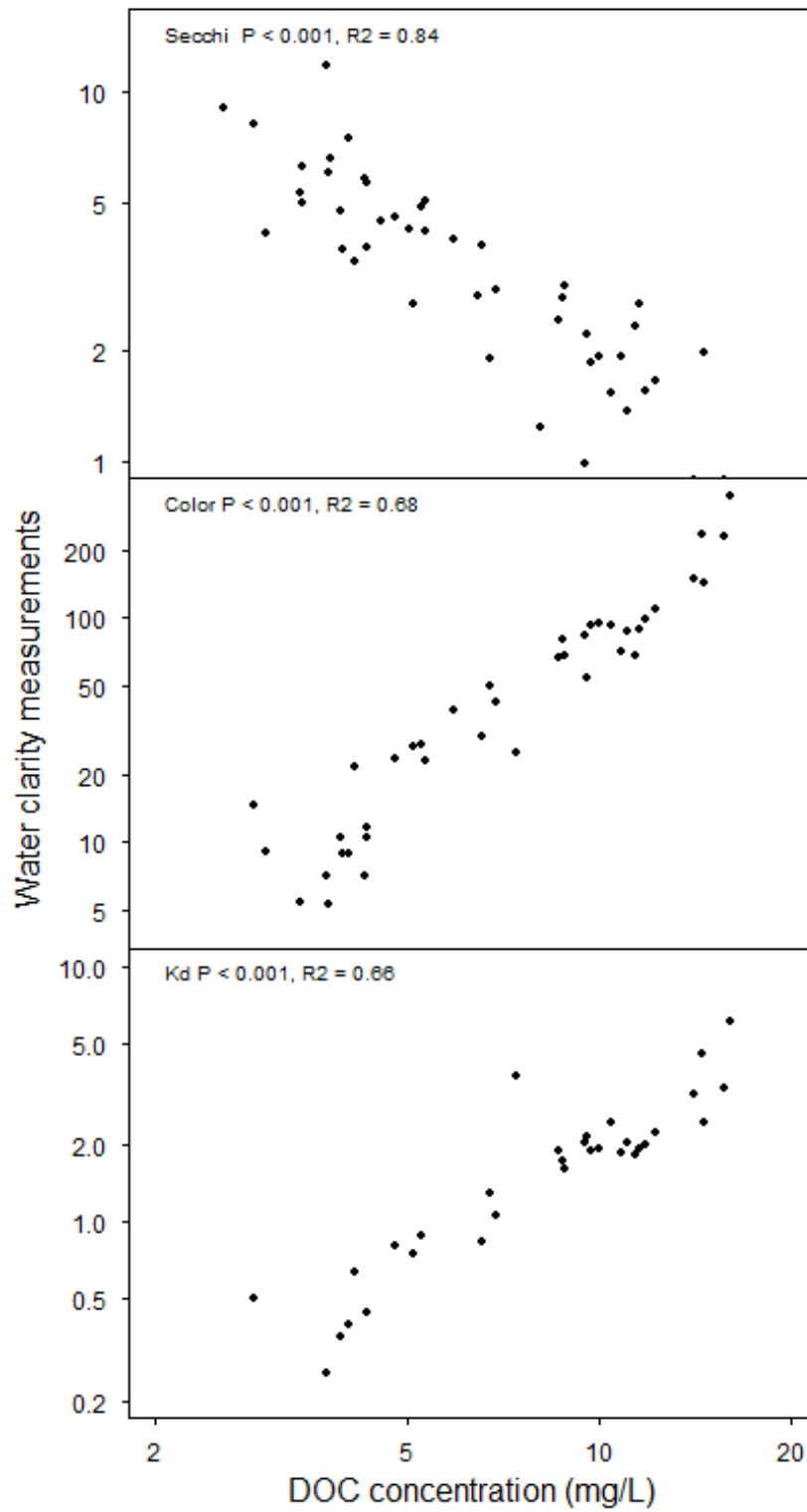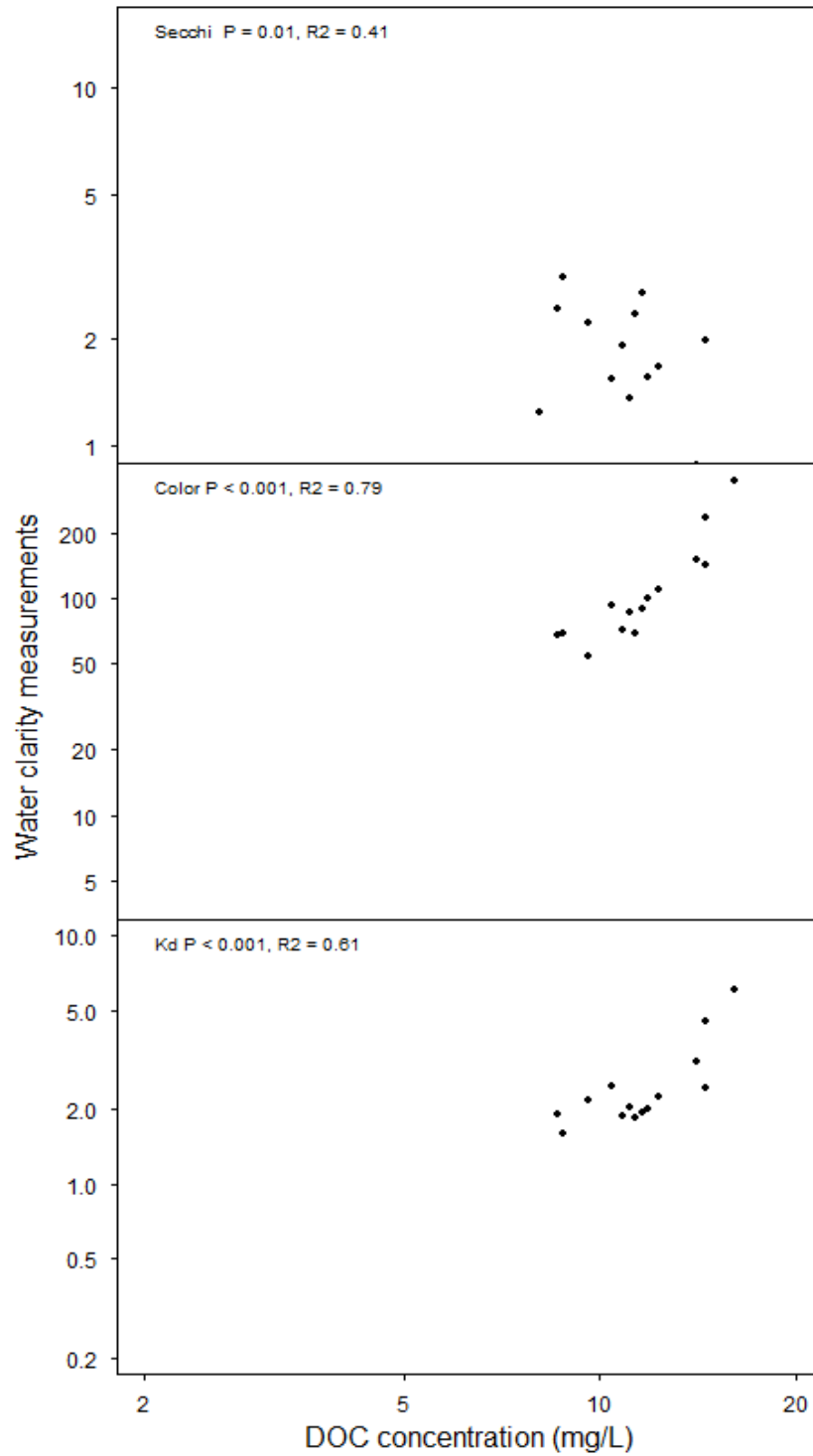
Fig. 8 Correlations between water clarity related measurements for Abitibi lakes where walleye has been sampled. The same scale as figure 7 has been conserved to show the lake clusters.

General conclusion

In this thesis, I examined how a changing DOC concentration could influence fish production in north temperate lakes with a main focus on the DOC-growth relation. The increase of terrestrial organic matter in aquatic ecosystem is affecting many important chemical, biological and chemical processes that are controlling fish community dynamics. Considering the complexity of these effects, it is hard to evaluate the possible resulting consequences on the whole-lake production and more precisely, on fish production. Previous observations mainly suggest that a reduction in fish production should be observed in darker, high-DOC lakes but the underlying mechanisms that are explaining this reduction are unclear. The first chapter of this thesis presented a review of the possible effects of an increase in DOC concentration on the characteristics of freshwater aquatic ecosystems, and how these effects could explain observed changes in fish production in these ecosystems, with a main focus on possible changes in fish growth rates. The second chapter examined the possible impact of changes in DOC concentration on the growth and relative abundance of three common North American fish species and how the importance of this impact varies for each species.

I observed strong but inconsistent inter-species changes in both early growth rate and relative abundance/biomass along with the increases in DOC concentration. Even if some weaknesses in the experimental design have been identified, many interesting observations have resulted from the large spatial ranges in higher DOC concentration covered for walleye and yellow perch. These observations are suggesting that the ultimate effect of a possible increase in DOC concentration on fish production could substantially differ between fish species and depending on the initial light conditions prevailing before perturbation.

Some authors have proposed that DOC concentration have been increasing in north temperate lakes in the past few decades (Evans et al. 2005; Monteith et al. 2007), and that this trend could turn to be more important in the next few years (Stasko et al. 2012). Given the dependence of primary and secondary productivity structure of

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northern, boreal lake ecosystems on organic carbon (Jones et al. 2012; Stasko et al. 2012), and the expected increase of terrestrial DOC inputs in these lakes along with more frequent and intense climatic perturbations (Driscoll et *al.*, 2003; Monteith et al. 2005; Stasko et al. 2012) a better understanding of the response of the whole lake food web to the observed and anticipated DOC-driven changes in water clarity and resources availability is of major importance for further studies (Finstad et al. 2014). Based on my observations, future research in this area should include better measurements of species-specific growth predictors (in addition to DOC), fish data from lakes covering larger DOC ranges and more reliable growth estimates.

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