ARTICLE

Experimental whole-lake dissolved organic carbon increase alters fish diet and density but not growth or productivity

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Abstract: Negative relationships between dissolved organic carbon (DOC) concentration and fish productivity have been reported from correlative studies across lakes, but to date there have not been experimental tests of these relationships. We increased the DOC concentration in a lake by 3.4 mg·L⁻¹, using a before–after control–impact design, to quantify the effects on the productivity and population structure of largemouth bass (*Micropterus salmoides*). Greater DOC reduced the volume of the epilimnion, the preferred habitat of largemouth bass, resulting in increased bass density. The likelihood that adult bass had empty diets decreased despite this increase in bass density; diet composition also changed. There was no apparent change in bass growth or condition. Overall, there was no net change in largemouth bass productivity. However, changes in young of year and juvenile recruitment and feeding success suggest the possibility that future effects could occur. Our results are the first to examine the effects of an increase in DOC on fish productivity through a 5-year temporal lens, which demonstrates that the relationship between DOC and fish productivity is multidimensional and complex.

Résumé : Des études corrélatives sur des lacs multiples ont fait état de relations négatives entre la concentration de carbone organique dissous (COD) et la productivité de poissons, mais aucun test expérimental permettant de valider ces relations n'a été proposé à ce jour. Nous avons accru la concentration de COD dans un lac de 3,4 mg·L⁻¹ et employé un schéma avant–après témoin–intervention pour quantifier les effets sur la productivité et la structure de la population d'achigans à grande bouche (*Micropterus salmoides*). Une plus grande concentration de COD s'est traduite par une réduction du volume de l'épilimnion, l'habitat privilégié des achigans à grande bouche, entraînant une augmentation de la densité d'achigans. La probabilité que des achigans adultes aient des régimes alimentaires vides a diminué malgré la densité accrue d'achigans; la composition des régimes alimentaires a également changé. La croissance et l'embonpoint des achigans ne présentent pas de changement apparent. Globalement, il n'y a pas eu de changement net de la productivité des achigans à grande bouche. Cependant, des modifications du recrutement de jeunes de l'année et de juvéniles et du succès d'alimentation indiqueraient que des effets futurs sont possibles. Nos résultats sont les premiers à examiner les effets d'une augmentation du COD sur la productivité de poissons dans une optique quinquennale, qui démontre que la relation entre le COD et la productivité de poissons est complexe et multidimensionnelle. [Traduit par la Rédaction]

Introduction

Dissolved organic carbon (DOC) concentrations vary widely across lake-rich landscapes, and many lakes in the Northern Hemisphere are increasing in DOC (Hanson et al. 2007; Monteith et al. 2007). This observed trend of DOC increase is occurring due to several mechanisms, some of which include changes in temperature, hydrological processes, land use, and declines in acid deposition (Freeman et al. 2001; Evans et al. 2005, 2006; Clark et al. 2010). These changes in DOC are responsible for fundamentally reshaping the chemical and physical characteristics of lakes and in turn the biological interactions of lake ecosystems (Jones 1992; Solomon et al. 2015).

Research over the past decade has highlighted the role that terrestrial inputs of DOC can play in influencing the productivity of lake food webs, from primary producers to fishes. At high DOC concentrations, DOC-related shading generally results in reduced whole-lake temperature, dissolved oxygen concentrations, and light availability (Houser 2006; von Einem and Graneli 2010; Read and Rose 2013; Solomon et al. 2015; Vasconcelos et al. 2016). These DOC-related changes have been associated with a decline in productivity at all lower trophic levels, including primary productivity (Ask et al. 2009; Seekell et al. 2015a, 2015b), benthic invertebrate biomass (Craig et al. 2015; Karlsson et al. 2015), and zooplankton production (Kelly et al. 2014). Reduction in productivity across the lower trophic levels can be expected to also affect the productivity of higher consumers, such as fish.

Fish productivity has been found to be reduced in lakes with higher DOC concentrations. This has been observed as declines in fish growth rates, catch per unit effort (CPUE), and overall production (Karlsson et al. 2009, 2015; Finstad et al. 2014; Benoît et al. 2016). A variety of proposed mechanisms could account for the negative relationship, including reduced food availability due to lower trophic-level production declines, potentially acting via constraints on life history strategies (Jones et al. 2012; Stasko et al.

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2012; Craig et al. 2017); shading-induced decreases in temperature and dissolved oxygen concentrations on their physiology and habitat availability (Jobling 1994; Stasko et al. 2012); and the effects of a reduced light climate on capture efficiency of prey by predators (Stasko et al. 2012; Solomon et al. 2015; Weidel et al. 2017). However, these findings have only been observed through spatial surveys, and the effects of DOC on fish productivity have not been observed through time.

While there is a consistent negative effect of DOC observed on food web and fish productivity in the spatially comparative studies described, there has been no temporal and experimental test of the relationship between DOC and fish productivity within a lake ecosystem. While offering insight on the broad relationships between DOC and productivity, spatial surveys or space-for-time substitutions cannot always accurately predict how a system will change over time (Pickett 1989; Kratz et al. 2003). This can be attributed to the environmental variability that arises with the spatial heterogeneity in comparative spatial surveys, which may mask nuanced and context-dependent mechanisms and effects (Houle et al. 1995; Hanson et al. 2007; von Einem and Graneli 2010; Monteith et al. 2015). Furthermore, the observable changes through time may be different than what is observed via spatial comparisons, since comparing the dynamics through a suite of stable-system lakes may be vastly different than the dynamics observed within a recently perturbed system through time (Pickett 1989; Carpenter et al. 1998; Kratz et al. 2003). Experimental temporal studies are useful for these reasons, since we can directly observe the mechanisms that may drive DOC-related effects on productivity, especially if these are effects only observable through a temporal lens.

In this study, we used a 5-year whole-lake experiment to test the effect of increased DOC on largemouth bass (*Micropterus salmoides*) in a north-temperate lake. We initially hypothesized that an increase in DOC concentration would reduce fish productivity. Our rationale was that DOC-induced reductions in the benthic and pelagic prey availability and fish habitat availability would lead to negative effects on fish productivity via changes in diet and reductions in growth, condition, and abundance (Karlsson et al. 2009; Finstad et al. 2014; Kelly et al. 2014; Craig et al. 2015; Benoit et al. 2016). However, results from the first 4 years of the whole-lake experiment unexpectedly showed that increases in DOC concentration resulted in increases in pelagic primary productivity (Zwart et al. 2016), zooplankton biomass (Kelly et al. 2016), and zoobenthos biomass (N. Craig, S.E. Jones, P.T. Kelly, B.C. Weidel, J.A. Zwart, and C.T. Solomon, unpublished data). This suggested an alternative hypothesis: that the increase in DOC could lead to *increased* productivity of fish. We tested these alternative hypotheses by quantifying the response of the largemouth bass population to the whole-lake DOC manipulation, in terms of habitat availability and usage, population size, volumetric density, recruitment, diet composition, stomach fullness, body condition, and growth.

Methods

Experimental whole-lake DOC manipulation

We conducted a 5-year whole-lake DOC manipulation experiment, using a before–after control–impact design, to test the effects of increased DOC concentration on fish and other components of lake food webs. Details of the experimental manipulation and its effects on other components of the food web are described in full elsewhere (Zwart et al. 2016; Kelly et al. 2016). In brief, the experiment was conducted on Long Lake, an 8.1 ha lake at the University of Notre Dame Environmental Research Center in Gogebic County, Michigan, USA. The lake is hourglass-shaped, with a mean depth of 3.8 m and a maximum depth of 14 m in similarly sized east and west basins that are connected by a shallower shelf. The lake is closed to public access. In the spring of 2011, we separated the lake into two basins with a permeable

nylon mesh barrier, which allowed for the transfer of water between the two basins while keeping the fish community isolated within each basin. We monitored the fish populations in each basin during the open water periods of 2011 and 2012 and then replaced the permeable barrier with an impermeable barrier made of high-density polyester weave. We continued to collect data in both the treatment and reference basins for 3 years following this manipulation, during the open-water periods of 2013–2015. Because the majority of the DOC load to Long Lake is via an ephemeral stream entering on the eastern shore, this caused an increase in the DOC concentration of the eastern (treatment) basin from 8.0 to 10.2 mg·L^{-1} and an increase in the difference in DOC concentration between the treatment and reference basins from 0.14 to 3.52 mg·L^{-1} (Zwart et al. 2016).

Fish responses to experiment

We used data on fish abundance, diets, growth rates, body condition, and depth distribution to understand the effects of our DOC manipulation on fish populations. We focused our analysis on largemouth bass because our sampling (>5000 individuals captured between 2011 and 2015 using multiple methods, including electrofishing, angling, and minnow traps) indicated that they comprise 97% of the fish assemblage in the lake and an even larger share of the fish biomass. Other species present include yellow perch (*Perca flavescens*), brook stickleback (*Culaea inconstans*), central mudminnow (*Umbra limi*), and northern redbelly dace (*Chrosomus eos*).

For each basin-year, we estimated abundance of adult (>200 mm total length) and juvenile (100–200 mm) bass using mark–recapture methods and abundance of young of year (YOY, <100 mm) using a minnow trap CPUE index. In early May and September of each year, we electrofished the entire shoreline of each basin on alternating nights using a boat electrofisher with pulsed DC (500–1000 V, 120 pulses·s^{-1}, 1.0–2.5 amps), for a total of four nights in each basin-year. Each fish >150 mm was tagged with a unique radio frequency identification tag inserted into the abdominal cavity. We supplemented the electrofishing mark–recapture data with additional data from monthly May–August angling efforts that were focused on sampling fish diets (see below). We used the continuous Schnabel method across all recapture events within each basin-year to estimate abundances of adults and juveniles (Schnabel 1938). We also calculated epilimnetic density for each basin-year–stage combination by dividing the abundance estimate by the mean epilimnetic volume for that basin-year. YOY bass abundance was estimated from 280 trap-nights of minnow trap effort in each basin-year, concentrated in two 7-day periods, the first occurring approximately in mid-May and the latter in mid-August. We assessed experimental effects on abundance and density by comparing 95% confidence intervals for abundance estimates.

We sampled bass diets in each basin approximately monthly from May through September in each year of the experiment, via nonlethal gastric lavage (Kamler and Pope 2001). While we did not collect diet samples from late fall to winter, bioenergetics models indicated that bass growth in Long Lake occurs almost entirely during the warm summer months. We collected at least 10 diets from each basin on each sampling occasion, for a total of nearly 900 adult diets and 100 juvenile diets over the course of the experiment. We examined the entire contents of each diet under a stereomicroscope, identified each diet item, and measured the body length of a subset of diet items to calculate dry mass from published regression relationships (Sage 1982; McCauley 1984; Sample et al. 1993; Benke et al. 1999; Ramcharan et al. 2001; Sabo et al. 2002; Baumgärtner and Rothhaupt 2003; Méthot et al. 2012). Unidentifiable diet items comprised <0.2% of the diets by mass. We classified diets with <1 mg dry mass as empty and used a logistic regression to examine how the probability of an empty diet varied as a function of basin, year, and fish length. For non-empty diets, we used linear regression to examine the relation-

ship between the same predictors and log-transformed diet mass, as well as analysis of similarities (ANOSIM) coupled with Welch t tests to test for changes in diet composition (Stewart-Oaten et al. 1992; Clarke 1993; Kelly et al. 2016).

We estimated bass growth rates based on annulus widths of otoliths from 261 fish (11–35 fish per basin-year). These fish were collected primarily during September electrofishing efforts (i.e., at the end of the growing season), although we also examined otoliths from mortalities that occurred at other times of year, ignoring incomplete annuli from present-year growth. We removed the sagittal otoliths, mounted them in epoxy resin, and sectioned them transversely. We then examined them under a compound microscope and measured annual increment widths along a radius drawn perpendicular to the growth bands along the proximo-dorsal edge of the sulcus. We used the mixed-effects model approach described by Weisberg et al. (2010) to test for treatment and age effects on growth rates while controlling for year and individual effects. We used a likelihood-ratio test to test for a treatment effect within a full and reduced version of the mixed-effect model, with the full model accounting for treatment and a reduced model that excludes it. We described fish condition using a population-level log-log regression of body mass on total length for all bass captured during September sampling. Using these log-log regressions, relative condition was calculated using methods described by Le Cren (1951), where the relative condition is represented as the quotient (W/W') of the mass of an individual bass (W) and the exponentiated predicted mass based on the log-log condition regressions (W'). Length and mass were measured for all fish handled during our abundance and diet sampling. We assessed experimental effects on relative condition by comparing 95% confidence intervals.

We conducted a small temperature–tagging experiment in June to July 2014 to examine the effect of DOC concentration on habitat use. In each basin, we attached temperature loggers (iButton DS1920; Maxim Integrated, San Jose, California, USA) to 20 bass >300 mm total length, following the methods of Bridger and Booth (2003). The loggers recorded temperature with a precision of 0.5 °C every 10 min for a maximum of 2 weeks. We estimated the swimming depth of each recaptured temperature-tagged bass (three in both the treatment and reference basins) by comparing the recorded temperature at bass swimming depth to high-frequency water temperature recorded from a vertically distributed chain of temperature sensors (HOBO Pendants; Onset Computer Corporation, Bourne, Massachusetts, USA) suspended from the lake surface in each basin. We used a Welch t test to test for differences between basins in mean swimming depth (Stewart-Oaten et al. 1992).

Results

Depth distribution, abundance, and volumetric density

The mean swimming depth of temperature-tagged bass was significantly shallower in the treatment basin than in the reference basin (0.45 and 0.89 m for treatment and reference, respectively; Welch $t_{3.2} = 4.3$, $p = 0.02$; Fig. 1). This difference mirrored the difference in thermocline depth during the period of the temperature tag study, which was 2.04 m in the treatment basin and 2.37 m in the reference basin (Zwart et al. 2016). None of the 9383 temperature observations across the six tagged fish across the two basins was lower than the epilimnetic temperature at that time, indicating that fish spent minimal, if any, time below the thermocline during the temperature tag study period. Overall temperature of the epilimnion was significantly lower in the treatment basin relative to the reference as a result of the manipulation, changing from being 0.26 °C warmer in the treatment premanipulation to 0.63 °C colder postmanipulation (Welch $t_{442.3} = -7.9$, $p < 0.01$; data from Zwart et al. 2016).

Fig. 1. Swimming depth of individual largemouth bass (light gray lines) significantly differed between the reference (A; $n = 3$) and treatment (B; $n = 3$) basins of Long Lake during summer 2014 (Welch $t_{3.2} = 4.3$, $p = 0.02$). The dashed horizontal lines indicate the mean swimming depth in each basin, the black lines indicate the 10 min interval thermocline depth estimates, and the solid gray horizontal lines indicate the mean thermocline depth in each basin during the temperature tagging study.
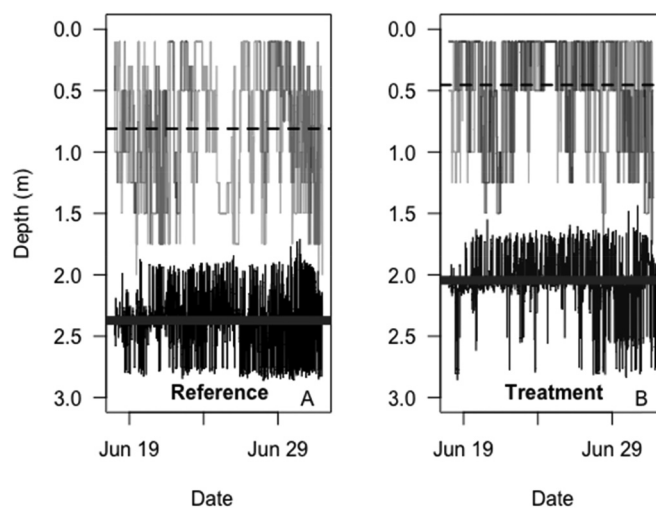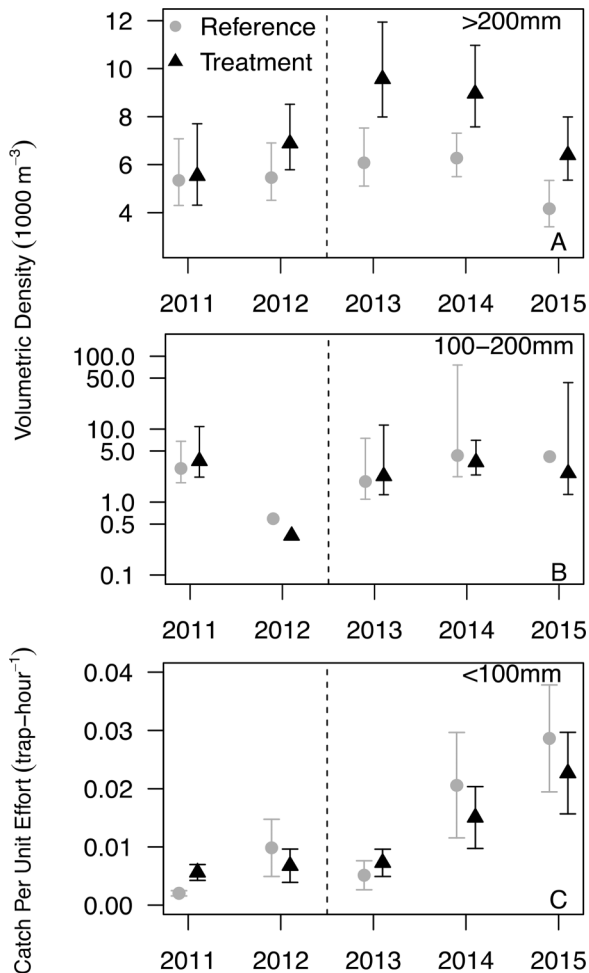

The volumetric density of bass in the treatment basin relative to the reference increased for adults, did not change for juveniles, and may have decreased for YOY (Fig. 2). Independent of treatment effects, the abundance and density of juvenile and YOY bass varied considerably from year to year (Table 1; Figs. 2B, 2C), including a considerable increase in YOY abundance in both basins in 2014 and 2015 (Fig. 2C). The increase in volumetric density of adults in the treatment basin was driven by both a weak relative increase in adult abundance (Table 1) and a decrease in the volume of available habitat as a result of the experimentally induced change in thermocline depth (Zwart et al. 2016). The epilimnion within the treatment basin shrank from 6.7×10^4 to 5.3×10^4 m³ due to the manipulation, while the reference shrank from 10.3×10^4 to 9.7×10^4 m³. The abundance of adult bass declined in both basins in 2015 (Table 1).

Largemouth bass diet

As a result of the DOC manipulation, the probability of an empty stomach was significantly higher for YOY and age-1 bass and significantly lower for large adult bass in the treatment basin relative to the reference (Fig. 3). For YOY and age-1 bass, this occurred because of an absolute increase in the probability of emptiness in the treatment basin in 2015. For adult bass, the change was mostly in the reference basin, where the probability of emptiness increased for large adult bass between 2013 and 2015. There was no change in the average diet biomass for non-empty diets (Fig. 4).

Diet composition for adult bass, but not juveniles, changed as a result of the manipulation (Fig. 5). Diets of adult bass, but not juveniles, became less similar between the treatment and reference basins as a result of the manipulation (adults: Welch $t_{16.3} = 2.6$, $p = 0.02$; Fig. 5A; juveniles: Welch $t_{11.9} = 0.9$, $p = 0.4$; Fig. 5C). This divergence of adult diets between the treatment and reference basins was driven by an increase in the abundance of *Chaoborus* in the diets in the treatment basin postmanipulation (Welch $t_{10.7} = 2.7$, $p = 0.02$; Fig. 6). The most important components of the diet were larval and pupal *Chaoborus* (comprising 18% to 98% of average juvenile diet across the basin-years and 14% to 85% of average adult diet) and the terrestrial adult phases of a variety

Fig. 2. Volumetric density of adult (A) and juvenile (B) bass and catch per unit effort of young of year (C) for each basin-year of the experiment. Error bars show 95% confidence intervals. Vertical dashed lines indicate initiation of the manipulation at the end of 2012. 2013–2015 represent manipulation years.

Fig. 3. Probability of an empty diet as a function of fish length for bass in each basin-year of the experiment. Solid lines show the fitted logistic regression model, and dashed lines show 95% confidence regions. The experimental DOC manipulation was initiated at the end of 2012, so 2013, 2014, and 2015 are manipulation years.

Table 1. Population estimates for juvenile and adult largemouth bass (with lower, upper 95% confidence limits) for treatment and reference basins.

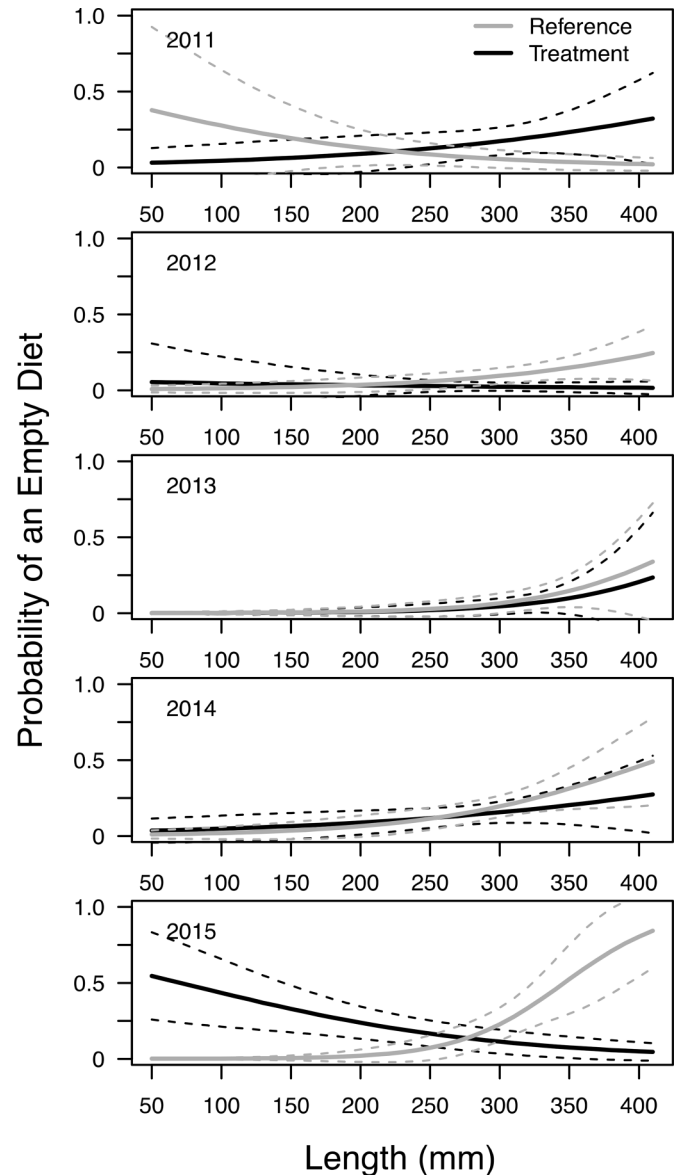|	Juvenile		Adult	
Year	Treatment	Reference	Treatment	Reference
2011	254 (153, 751)	275 (175, 647)	385 (300, 536)	508 (409, 673)
2012	22	65	439 (369, 543)	602 (498, 761)
2013	113 (63, 566)	182 (104, 713)	477 (398, 595)	579 (486, 717)
2014	189 (126, 177)	409 (210, 7146)	480 (406, 588)	592 (519, 690)
2015	135 (69, 2361)	430	348 (291, 434)	427 (350, 548)

Note: Confidence intervals could not be determined for juveniles in some years due to a lack of recaptures.

of insects (comprising 0% to 76.5% of average juvenile diet across the basin-years and 9.8% to 77.4% of average adult diet), including Ephemeroptera, Trichoptera, Coleoptera, Arachnida, and Hymenoptera (Figs. 5B, 5D).

Growth and condition

Growth rate and condition of adult, juvenile, and YOY bass showed no response to the experimental treatment (Fig. 7). There were no significant treatment effects on growth rates for fish of all age classes (Figs. 7A–7D; likelihood-ratio test p = 0.90). Otolith width increments were more constrained for age-0 fish, and be-

came more variable with greater age (Figs. 7A–7D). There was no change in specific condition for fish of all age classes (Figs. 7E–7H).

Discussion

Before initiating our experiment, our hypothesis — based on published relationships between DOC and food web productivity in spatial surveys — was that an increase in DOC would lead to reduced fish productivity. After observing the unexpected effects of the experiment on primary and secondary productivity (Kelly et al. 2016; Zwart et al. 2016; N. Craig, S.E. Jones, P.T. Kelly, B.C. Weidel, J.A. Zwart, and C.T. Solomon, unpublished data), we entertained the alternative hypothesis that the increase in DOC would lead to increased fish productivity. In fact, what we observed was something in the middle — relatively little change in fish productivity as a result of the manipulation, at least to date. The DOC manipulation led to a reduced largemouth bass habitat space during the stratified season due to shading-induced reduc-

Fig. 4. Mean dry mass of bass diet contents for large adult (A), juvenile (B), and YOY (C) fish in each basin-year. Points are point estimates from fitted regression model, and error bars indicate 95% confidence intervals. Vertical dashed lines indicate initiation of the manipulation at the end of 2012. 2013–2015 represent manipulation years.
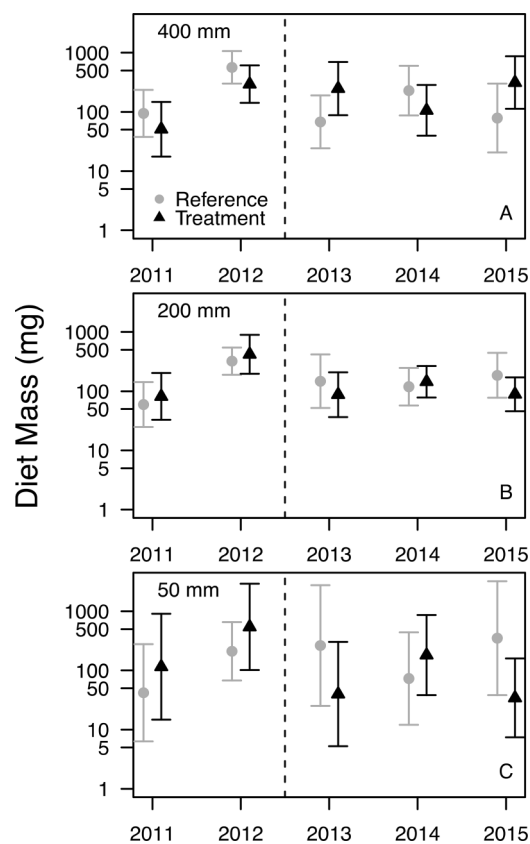
tion of epilimnetic volume (Fig. 1). The relative increase in abundance and reduction in stratification depth increased epilimnetic volumetric density of adults (Fig. 2A). Despite an increase in the density of the adult bass, we found that the adult bass in the treatment had an increased likelihood of diet fullness (Fig. 3), as well as an increase in *Chaoborus* in their diets (Fig. 6), which resulted in a change in their diet composition (Fig. 5). These changes, however, did not change adult growth or condition (Fig. 7) in the treatment basin.

Fish productivity and food web effects

Previous studies have found an overall negative relationship between DOC and fish productivity that is thought to be related to the light attenuating property of DOC. Results from spatial surveys have found decreased fish growth rates, lifetime fecundity, CPUE, and production in lakes high on the DOC spectrum (Karlsson et al. 2009, 2015; Finstad et al. 2014; Benoît et al. 2016; Craig et al. 2017). Reduced fish growth and productivity can be attributed to DOC's shading-related declines in temperature and dissolved oxygen concentrations (Houser 2006; Stasko et al. 2012; Zwart et al. 2016), which are important in determining the volume and quality of available habitat space. Reduced visual light environments can also reduce fish growth and productivity (Karlsson et al. 2009; Solomon et al. 2015), by influencing predator–prey interactions (such as prey detection and foraging efficiency) and basal productivity that support higher trophic levels (Stasko et al. 2012; Kelly et al. 2014; Craig et al. 2015; Weidel et al. 2017). However, in our experimental system, any potential negative effects on largemouth bass through these mechanisms were unobserved,

opposite of spatial surveys, or had an insignificant impact on fish growth and productivity.

While our results are apparently contradictory to previous cross-system surveys, they may be more consistent with the recent recognition that the concurrent export of DOC and limiting nutrients to lakes may actually increase basal production (Kissman et al. 2013; Solomon et al. 2015) and subsequently boost fish production under moderate browning scenarios (Finstad et al. 2014). Food web changes that we observed as a result of the DOC manipulation in Long Lake follow this predicted positive response. Gross primary production increased in the treatment basin (Zwart et al. 2016), with a subsequent increase in zooplankton abundance and density. Benthic invertebrate biomass increased in the metalimnion of the treatment basin, but did not significantly change within the epilimnion or the hypolimnion (N. Craig, S.E. Jones, P.T. Kelly, B C. Weidel, J.A. Zwart, and C.T. Solomon, unpublished data). The increase in zooplankton biomass may have led to an increase in the abundance of planktivorous *Chaoborus* within the treatment basin, which explains the higher *Chaoborus* abundance in the adult largemouth bass diets (Fig. 6). The increase in *Chaoborus* may be responsible for the change in adult largemouth bass stomach fullness (Fig. 3) and diet composition (Fig. 4A). While there was no direct observation of an increased density of *Chaoborus* in Long Lake (Kelly et al. 2016), this could be due to an under-sampling of *Chaoborus* due to zooplankton sampling occurring during the day when *Chaoborus* are normally benthic (LaRow 1968; Kelly et al. 2016) or due to intensive predation by the bass. These overall increases in food web productivity may have supported fish productivity through a bottom-up effect, relieving the bass community from the negative effects of DOC-related shading on the availability and quality of habitat space that resulted in no net changes to the productivity of the bass to the increase in DOC.

The potential for an increase in bottom-up support of the bass population via the pelagic gross primary production – *Chaoborus* mechanism may have been facilitated by the relatively poor availability of benthic prey in Long Lake. Benthic invertebrates are generally an important food source for fishes in small to medium-sized lakes (Vander Zanden and Vadeboncoeur 2002). In Long Lake, benthic invertebrates in average juvenile and adult diet masses did not change as a result of the manipulation (annual means between 1% and 13%), with the dominant diet items being terrestrial invertebrates (annual means between 0% and 74%) and *Chaoborus* (annual means between 14% and 98%). This may have been caused by a fairly limited benthic habitat space (Fig. 1), as well as the high densities of the largemouth bass (Fig. 2), resulting from Long Lake being closed to public access and being almost entirely dominated by bass. As generalist feeders, largemouth bass tend to exhibit optimal feeding behaviour, with a preference toward higher-quality prey items (Hodgson and Kitchell 1987). A significant increase and shift toward *Chaoborus* as a diet item within the treatment may indicate that *Chaoborus* represents the best available prey item within the experimental lake. With the increased basal productivity in the treatment basin (Kelly et al. 2016; Zwart et al. 2016) and the increase in *Chaoborus* abundance, the available prey pool in the treatment may have increased, resulting in better diet quality and allowed for the offset of any negative effects of DOC on habitat space.

Our results also suggest that largemouth bass may be able to adapt to browning waters. When placed under varying stressors, largemouth bass have been shown to adapt accordingly to mitigate adverse effects to their physiology, through behavioural changes in their habitat space occupancy and prey selectivity (Schindler et al. 1997; Hasler et al. 2016). Temperature is known to be a key determinant of largemouth bass movement and habitat preference, with bass actively seeking out higher water temperatures to fit within their thermal optimum (Brown et al. 2009; Peat et al. 2016). Population density and poor prey availability has been

Fig. 5. Diet composition for adult (>200 mm; panels A and B) and juvenile (100–200 mm; panels C and D) bass in the reference and treatment basins between 2011 and 2015. In panels A and C, each point shows the dissimilarity in diet composition between the treatment and reference basins on a given date. This dissimilarity is the ANOSIM R statistic, which varies from –1 to 1; values <0 indicate greater diet dissimilarity within a basin than between basins, values near 0 indicate equal within- and between-basin dissimilarity, and values >0 indicate greater dissimilarity between basins than within basins. Diet dissimilarity between the basins increased in the postmanipulation period (2013–2015) for adult bass (A; Welch t test, $p = 0.02$) but not for juvenile bass (C; $p = 0.41$). Panels B and D show the contribution of several diet item categories to the total dry mass of the mean diet in each year for the reference basin (REF) and treatment basin (TRT). Unknown vertebrates, pelagic invertebrates, and small zooplankton each represented <0.2% of the diets and were excluded from these figures. Vertical dashed lines indicate initiation of the manipulation at the end of 2012. 2013–2015 represent manipulation years.
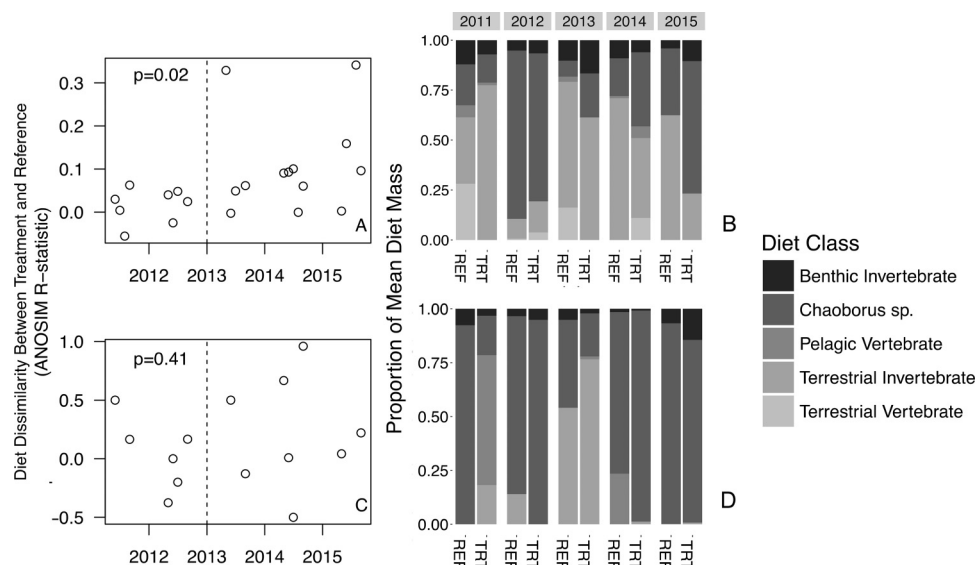
Fig. 6. Dry mass of *Chaoborus* spp. in adult largemouth bass diets in the treatment and reference basins. Data are monthly means (with 95% confidence intervals). Vertical dashed line indicates initiation of the manipulation at the end of 2012. 2013–2015 represent manipulation years.
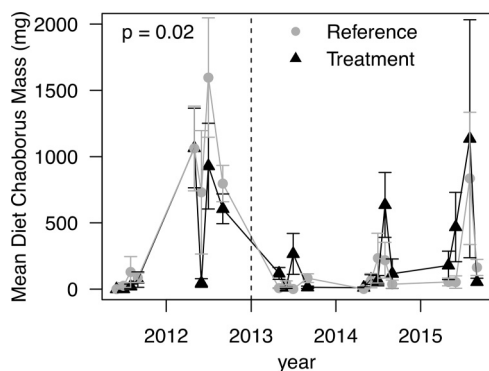
observed to have a significant effect on largemouth bass prey selectivity and specialization (Schindler et al. 1997; Hodgson et al. 2008). In terms of predator behaviour, Stasko and colleagues (2015) have found that with increasing water colour, smallmouth bass (*Micropterus dolomieu*) expand their niche size, possibly due to a major change in prey selectivity. While our observations on habitat selection is limited in both sample size and study duration, we observed a behavioural response to the DOC manipulation through optimal habitat selection (Fig. 1). This observation, however, could be stronger if we had data available about the largemouth bass usage of the hypolimnion. We also observed changes to their diet composition and stomach fullness as a result of the DOC manipulation (Figs. 3, 5, 6). This may provide evidence that the increased DOC did deteriorate habitat conditions for the largemouth bass, but behavioural adaptations allowed them to mitigate the adverse effects of the changes in temperature and

dissolved oxygen that decreased the availability and quality of their habitat space.

Space-for-time substitution versus experimental studies

One explanation for the discrepancy between our results and previous findings of negative responses between fish production and DOC is that space-for-time substitutes are not adequate in defining the transient mechanisms that dictate the DOC-related responses on lake productivity. Spatial surveys comprise the majority of studies that consider the effect of DOC on lake productivity (Karlsson et al. 2009; Kelly et al. 2014; Seekell et al. 2015a). Our results suggest that inferences based on spatial surveys alone are not suited to describe temporal changes in response to a perturbation (Carpenter 1998; Kratz et al. 2003). Recently perturbed systems, such as Long Lake, may go through transient dynamics, which lead to fluctuating responses of productivity within the lake as it approaches a state of dynamic equilibrium (Pickett 1989). Furthermore, environmental variability and interactions among lake shape, size, watershed, surrounding vegetation, and geographic regions may obscure DOC effects on productivity when one considers results from spatial surveys (Houle et al. 1995; Hanson et al. 2007; von Einem and Graneli 2010; Monteith et al. 2015).

Whole-lake experiments offer a different perspective than spatial surveys for the previously mentioned reasons. While having to account for transient dynamics, whole-lake experiments allow for direct ecosystem responses to a selected perturbation that can be measured without having to account for environmental variability, which typically arises when comparing lakes across a heterogeneous landscape (Carpenter 1998). Whole-lake experiments also allow for the direct measurement of the mechanistic responses of the ecosystem to the perturbations (Carpenter 1998). While spatial surveys are important in understanding the general responses to a perturbation on a wide range of lakes, experimental observations may give a better understanding of mechanistic responses to perturbations and a more direct understanding of

Fig. 7. Growth (width of otolith annulus; panels A through D) and relative condition (panels E through H) of largemouth bass in the treatment and reference basins. Each panel represents an age class, as indicated at the bottom-left of the panel. Missing boxplots (panel F 2012; panel G 2013) occurred when no fish of the age class in question were caught during that year. Boxplots show the 5th, 25th, 50th, 75th, and 95th percentiles. Sample size is displayed (panels A through D) as numbers above boxplots. Vertical dashed lines indicate initiation of the manipulation at the end of 2012. 2013–2015 represent manipulation years.
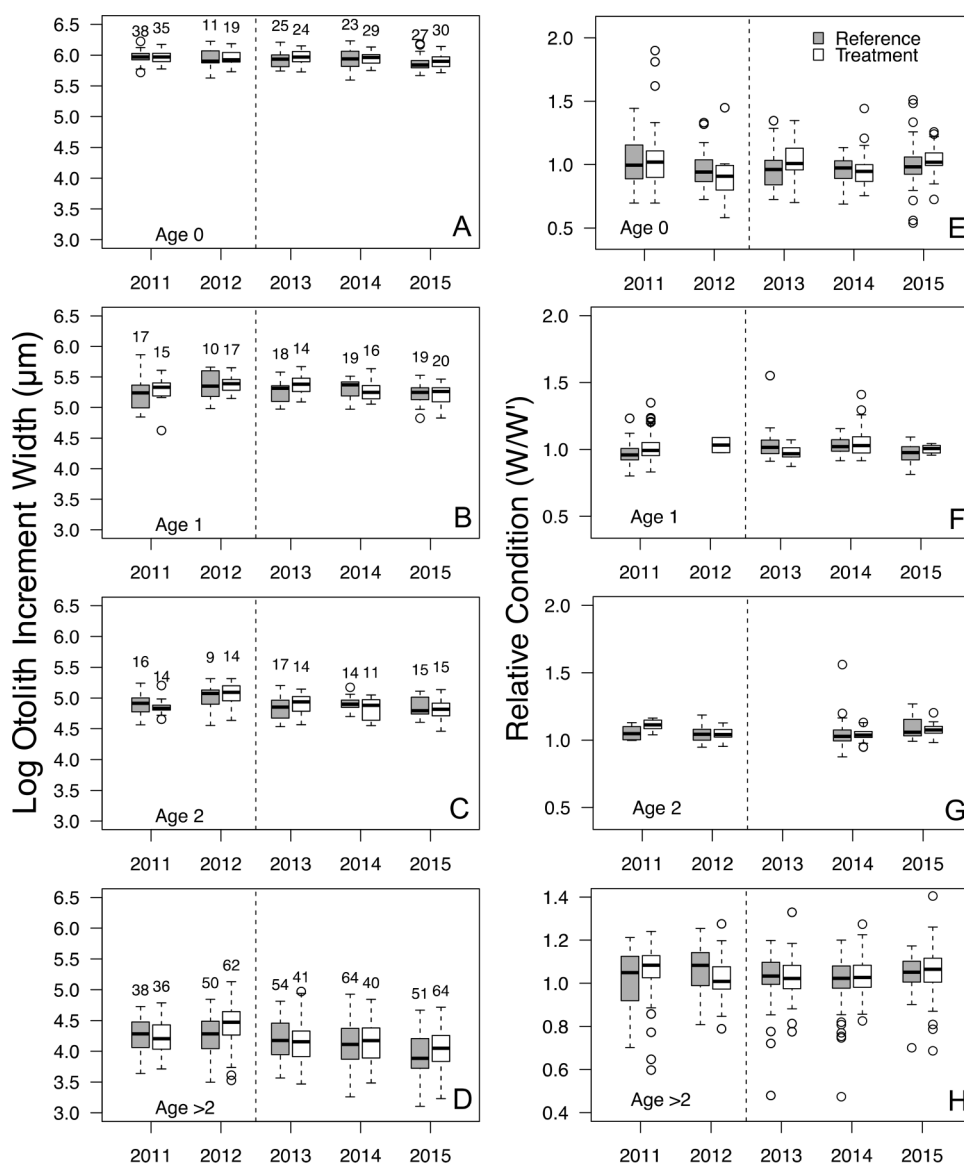
cause–effect relationships. These inherent differences between spatial studies and whole-lake experiments may lead to different interpretations of results and observations of the same environmental change in question.

Long Lake, the DOC gradient, and future population dynamics

Within the cited space-for-time studies that looked at the effects of DOC on fish production, the total DOC gradient ranged from approximately <1 to 22 mg·L⁻¹ (Karlsson et al. 2009, 2015; Finstad et al. 2014; Benoît et al. 2016). Over this large DOC range, a strong negative effect of DOC may become apparent. However, in the Long Lake experimental system, the DOC concentration in the treatment basin shifted from 8.0 to 10.2 mg·L⁻¹, resulting in an increased difference of the mean DOC concentration between the treatment and reference basins from 0.1 to 3.5 mg·L⁻¹. Within this relatively narrow DOC gradient, it may be difficult to observe the negative effects of DOC on fish productivity, despite major

changes in habitat and lower trophic levels. This may imply that a greater increase in the DOC concentration within the treatment basin may lead to the expected negative effect on fish productivity.

There is some evidence that the experimental increase in DOC in Long Lake is beginning to lead to decreased fish productivity and changes in size-structure dynamics and that a longer time period may be required to observe DOC-induced effects on the bass population. Within the last 3 years of our experimental treatment, we observed shifts in the population structure. This was seen in the recruitment estimates, which showed a considerable increase in YOY CPUE (Fig. 2C) and juvenile bass abundances (Table 1) in both basins for 2014 and 2015, but at a smaller magnitude in the treatment basin. Population estimates show that adult bass are decreasing in both the reference and treatment basins in 2015 (Table 1). A significant change in diet fullness was observed for 2015 (Fig. 3), where the probability of an empty stomach was significantly higher for treatment YOY and juvenile bass and sig-

nificantly lower for large adult bass. These changes show that YOY and juvenile bass are increasing within both basins of Long Lake, possibly due to the decrease in adult abundances. In conspecific cannibalistic fish populations, like largemouth bass, die-offs of adult fish can lead to a spike in YOY due to a release from predatory pressure (Post et al. 1997; Persson et al. 2000). However, the YOY and juvenile bass may be hindered within the treatment basin due to the DOC-related changes in habitat space via changes in dissolved oxygen and temperature conditions, which may explain the reduced YOY CPUE and diet fullness. If the experiment were to continue for a longer duration, we may eventually see these negative effects on the YOY and juvenile bass extend into adult populations.

While we observed both positive and negative effects of an increase in DOC on conditions for fish in our experimental lake, we found no detectable changes in the productivity of the fish community. Contrary to spatial surveys, we found that fish productivity was not affected by the increase in DOC, possibly due to an increase in the available nutrients, and subsequently food resources (namely *Chaoborus*) that may have acted as a subsidy for adult largemouth bass, negating any adverse effects that DOC-induced shading has on habitat space and consequently physiological conditions. While we did not observe any noticeable responses to an increase in DOC in the productivity and growth of the bass, changes in size structure and competition between size classes may result in future reductions in productivity. While on a narrow DOC gradient, our experiment is the first to observe the effects of increasing DOC on fish productivity through time, and our results underline the fact that while spatial surveys are important in understanding generalizable large-scale relationships between DOC and fish productivity, the actual interactions that govern these relationship within a lake across time are uniquely complex and context-dependent. The relationship between DOC and fish productivity is not simple or linear when observing it through time, and further investigation is required to fully understand the mechanisms that drive DOC-related changes in fish productivity.

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