Light climate and dissolved organic carbon concentration influence species-specific changes in fish zooplanktivory

Brian C. Weidel, Katherine Baglini, Stuart E. Jones, Patrick T. Kelly, Christopher T. Solomon & Jacob A. Zwart

SIL

Taylor & Francis
Taylor & Francis Group

Check for updates

Light climate and dissolved organic carbon concentration influence species-specific changes in fish zooplanktivory

Brian C. Weidel,[a][§] Katherine Baglini,[b] Stuart E. Jones,[b] Patrick T. Kelly,[b] Christopher T. Solomon,[c] and Jacob A. Zwart[b]

[a]U.S. Geological Survey, Great Lakes Science Center, Lake Ontario Biological Station, Oswego, NY, USA; [b]Department of Biological Sciences, University of Notre Dame, Notre Dame, IN, USA; [c]Department of Natural Resource Sciences, McGill University, Sainte-Anne-de-Bellevue, QC, Canada

ABSTRACT

Dissolved organic carbon (DOC) in lakes reduces light penetration and limits fish production in low nutrient lakes, reportedly via reduced primary and secondary production. Alternatively, DOC and light reductions could influence fish by altering their visual feeding. Previous studies report mixed effects of DOC on feeding rates of zooplanktivorous fish, but most investigators tested effects of a single concentration of DOC against clear-water, turbid, or algal treatments. We used a controlled laboratory study to quantify the effects of a DOC gradient (3–19 mg L^{-1}) on average light climate and the zooplankton feeding rate of 3 common, north temperate fishes. Light availability, which was inversely related to DOC concentration, had a positive and linear effect on zooplankton consumption by juvenile largemouth bass (*Micropterus salmoides*) and bluegill (*Lepomis macrochirus*), explaining 22% and 28% of the variation in consumption, respectively. By contrast, zooplankton feeding rates by fathead minnow (*Pimephales promelas*) were best predicted by a nonlinear, negative influence of light ($R^2 = 0.13$). In bluegill feeding trials we found a general trend for positive selection of larger zooplankton (Cladocera and Chaoboridae); however, the light climate did not influence the selection of prey type. Largemouth bass selected for larger-bodied zooplankton, with weak evidence that selectivity for large Cladocera changed from negative to neutral selection based on electivity values across the light gradient. Our results suggest that the effect of DOC on the light climate of lakes may directly influence fish zooplanktivory and that this influence may vary among fish species.

Introduction

Lake dissolved organic carbon (DOC) concentration is primarily controlled by inputs of terrestrial derived organic material (Wilkinson et al. 2013) and plays a fundamental role in structuring lake ecosystems, serving as both a nutrient resource and a physical regulator of light and temperature by absorbing solar radiation (Prairie 2008; Solomon et al. 2015). DOC concentration varies widely among lakes, and the fact that lake concentrations have been changing over the past several decades in north temperate and boreal regions emphasizes the importance of understanding its role in regulating fishes and lake food webs (Roulet and Moore 2006; Hanson et al. 2007; Monteith et al. 2007). Recent work suggests that the DOC concentration and subsequent light changes are an important driver of fish production, reducing production as DOC concentration increases (Karlsson et al. 2009; Stasko et al. 2012). A commonly suggested bottom-up

mechanism for this pattern posits that light reductions reduce primary production and invertebrate consumer production, which ultimately limits fish production. Mechanistic simulation models and empirical studies have both demonstrated that bacterial, algal, and invertebrate production can be strongly limited by terrestrial inputs and increasing DOC concentration (Ask et al. 2009; Jones et al. 2012). Alternatively, DOC may directly influence fish populations by regulating the ambient light climate, which may govern the feeding ability of some fishes.

The optical properties of water can regulate fish feeding behavior and efficiency (Abrahams and Kattenfeld 1997). Most studies evaluating how optical conditions influence fish feeding have focused on the role of turbidity, where suspended particles scatter ambient light and change contrast conditions between fish prey. Turbidity has been shown to have both positive and negative influences on fish feeding by enhancing the contrast between food items

and the environment in larval fish but reducing light and search volume of larger fishes (Vinyard and O'Brien 1976; Utne-Palm 2002). Increased turbidity has also been demonstrated to impact visual detection of different sized prey, where larger items become more difficult to see in turbid environments (contrast degradation theory; De Robertis et al. 2003). Colored dissolved organic material (CDOM), which is highly correlated with DOC (Tranvik 1990), can also influence the light environment of fishes and has the potential to influence feeding behavior. In contrast to suspended particles, DOC does not scatter light, but rather absorbs light and reduces the overall light intensity (Morris et al. 1995). The role of DOC or humic substances influencing fish feeding has only been recently explored, such as in Jönsson et al. (2013) who demonstrated that suspended particles and humic substances had differing effects in degrading the visual environment of feeding fishes.

The few previous studies that investigated the effect of DOC on fish feeding have yielded mixed results. Much of the research has focused on predator–prey interactions between piscivores and prey fishes. For instance, Ranåker et al. (2012) found that reaction distance in pike (*Esox lucius*) and roach (*Rutilus rutilus*) declined with increasing light attenuation and noted that the influence of algae and solids was stronger than that of DOC treatments. In one of the few studies experimenting with zooplanktivorous fishes, Stasko et al. (2012) found zooplanktivory by juvenile roach (15–20 mm) was slightly decreased in DOC and algae treatments relative to feeding in clear water, but reductions were not statistically significant. Experiments that quantify rates of zooplanktivory along a DOC gradient are absent from the literature, but these studies would be important in determining appropriate functional forms and their parameterization for inclusion in ecological models.

We sought to quantify the role of DOC-mediated light attenuation in controlling fish zooplanktivory for largemouth bass (*Micropterus salmoides*), bluegill (*Lepomis macrochirus*), and fathead minnow (*Pimephales promelas*). We chose these fishes because they are common in this region, were readily available, included diverse feeding strategies, and represented different ontologies with respect to zooplantivory. We hypothesized that DOC-induced reductions in light climate would linearly reduce zooplanktivory for particulate feeders (largemouth bass and bluegill), whereas zooplanktivory in fathead minnows, which employ both particulate and filter feeding strategies (Hambright and Hall 1992), would not respond to light climate changes. We also evaluated whether nonlinear models provided a better fit to observed patterns, and finally we hypothesized that the influence of increased DOC and reduced light would have a disproportionately greater effect on larger zooplankton prey consumed. To evaluate our hypotheses we created a gradient of light climates via manipulation of DOC concentrations in laboratory tanks and measured the amount of zooplankton consumed by our 3 species across those gradients.

Methods and materials

Fish feeding trials were conducted in 1186 L of natural lake water in indoor tanks at the University of Notre Dame Environment Research Center, using common north temperate lake fishes and natural lake zooplankton assemblages. Source water for each tank was from nearby Tenderfoot Lake, with a DOC concentration of 12.88 mg L^{-1} (color $g_{440} = 3.85$). To attain target DOC concentrations we added measured aliquots of commercially available concentrated terrestrial DOC (Super Hume, UAS of America Inc., Lake Panasoffkee, FL), which is similar to the terrestrial DOC exported to lakes (for more in-depth description of SuperHume product, see Lennon et al. 2013). DOC concentrations were randomly assigned to tanks. The range of DOC concentrations in our experimental tanks (3–19 mg L^{-1}) was chosen to be similar to that reported in a recent multi-lake survey that spanned natural DOC concentrations for lakes in this region (5.4–25.9 mg L^{-1}; Kelly et al. 2014). We used average light climate instead of DOC as the explanatory variable influencing fish feeding because incoming light varied due to the arrangement of tanks and overhead fluorescent lighting in the experimental lab (surface light [I_0] range 7.13–10.45 μmol m^{-2} s^{-1}). Fluorescent lights were T12 Cool White fluorescent lamps, emitting in the 4100 °K portion of the color spectrum. The color spectrum of natural light changes depending on time of day and weather conditions, ranging from ~6500 °K during an overcast day to ~10 000 °K near the equator. The lamps used in this study emitted a color spectrum of light more characteristic of that at sunrise/sunset, meaning that tanks were likely receiving less blue light than would be experienced in a natural lake exposed to daytime sunlight, and our results may be accentuated because blue light penetrates further into the water column. Light (400–700 nm) was measured with a Licor LI-250A and an attached LI-192 underwater quantum sensor just above the surface of the water for ambient light, just under the surface and at depths of 22.8 cm and 45.7 cm. Light extinction coefficient (K_d) was calculated by fitting a best fit line to the 3 measured tank light levels using equation 1:

$$I_z = I_0 e^{(-Kd*z)} \tag{1}$$

where I_z is light at depth z, and I_0 is incoming light just above the surface of the water. To calculate the average

light climate we used the fitted models (equation 1) to integrate light over the entire depth of the tank (45.7 cm) and divided by depth of the tank.

Juvenile bluegill and young-of-year largemouth bass used in feeding trials were collected from natural populations via minnow or fyke netting in Tenderfoot Lake on the University of Notre Dame Environmental Research Center (UNDERC) in Michigan's Upper Peninsula. Fathead minnows were purchased from a bait shop in Land O' Lakes, Wisconsin, where they were held indoors in glass tanks receiving ambient light conditions within the store. Typically, the bait shop did not give food to the minnows because turnover of the minnows was quick; however, if the minnows were fed they received pelleted fish food. The bait shop purchased the minnows from multiple licensed dealers, but it was not possible to specify from which aquatic environment the licensed dealers acquired the minnows. Fish collection and care followed approved institutional animal care and use protocols and state of Michigan collection protocols. All fish were transferred to 1186 L holding tanks, acclimated to lab conditions for 1–3 days, and fed live zooplankton collected daily from Tenderfoot Lake.

For each species we conducted 3 feeding trials on different days, and within each feeding trial 4 different tanks (volume = 1186 L, tank diameter = 181 cm, water depth = 45.7 cm) were used, each varying in DOC concentration. In the bluegill and fathead minnow trials, 10 individual fish were added to each tank, whereas only 3 individual largemouth bass were used per tank because they were larger (Table 1). Before the feeding trials, experimental

tanks were filled with filtered lake water to remove zooplankton, and measured aliquots of commercially available concentrated terrestrial DOC were added to achieve a desired final DOC concentration. Fish were randomly selected from the population, separated, and starved for 24 hours. Starved fish were then randomly selected, added to the feeding trial tanks, and allowed to acclimate without food in the colored water for 2 hours. A natural assemblage of live zooplankton collected daily from Tenderfoot Lake were added to each tank. For each experimental tank, zooplankton were added in the approximate density found in Tenderfoot Lake. Three replicate zooplankton tows (80 μm mesh, 30 cm diameter) were collected from Tenderfoot Lake at ~6 m to the surface and combined so that zooplankton density in the feeding trial tanks would be similar to that in the lake volume sampled (1270 L). An additional zooplankton tow from Tenderfoot Lake was preserved each trial day to estimate the starting density and taxonomic composition of zooplankton provided in the feeding trials. Tanks were drained after each trial, so each feeding trial began with new water, DOC supply, and zooplankton.

Experimental fish were allowed to feed for 2 hours before they were netted and euthanized with an overdose of tricaine methanesulfonate (MS-222). Gut contents of all fish from each tank were dissected, preserved, identified, and enumerated for bluegill and largemouth bass; for fathead minnows, mastication prevented individual zooplankton enumeration or identification, so we instead dried and weighed the gut contents. The gut was defined as extending from the buccal cavity to the pyloric caeca. Any fish that appeared sick or disoriented were removed from the feeding tanks and euthanized with an overdose of MS-222; those data were not included in analyses (removed fish were 9% of bluegill, 20% of fathead minnows, and 0% of largemouth bass trials). Zooplankton diet items were categorized into 4 taxonomic groupings: (1) small Cladocera, which included *Bosmina* sp. and *Chydorus* sp.; (2) Copepoda, which were primarily Cyclopoida; (3) large Cladocera, which included *Daphnia* sp., *Ceriodaphnia* sp., *Holopedium* sp., and *Diaphanasoma* sp.; and (4) Chaoboridae.

To estimate the proportion of each live zooplankton group added to the tanks, the preserved lake zooplankton samples were subsampled and counted using a Bogorov counting chamber and a stereo microscope. We counted 1000 randomly sampled individuals, or all individuals if <1000 were present, from each sample to estimate the proportion by number for each of the 4 taxonomic groupings. Subsamples were extrapolated to estimate abundance of whole samples. We quantified diet electivity between largemouth bass and bluegill diets and the proportion of zooplankton groups added to the tanks using the E* index

Table 1. Fish and tank conditions for experimental feeding trials. Fish total length, tank temperature, and dissolved oxygen concentration represent the mean and standard deviation for all tanks in a given trial. The number of fish in a given trial excludes those removed individuals that appeared sick or disoriented. Tanks were 1186 L.

Species	Trial ID	# of tanks	total # of fish	Fish length (mm)	Tank temperature (°C)	Dissolved oxygen (mg L^{-1})
Bluegill	1	4	33	46.0 (4.9)	20.5 (0.3)	8.1 (0.1)
Bluegill	2	4	35	47.4 (3.6)	20.9 (0.1)	8.0 (0.0)
Bluegill	3	4	37	45.5 (4.4)	21.1 (0.1)	7.9 (0.2)
Largemouth bass	4	4	12	73.8 (10.1)	20.4 (0.2)	8.1 (0.1)
Largemouth bass	5	4	12	69.6 (6.3)	19.8 (0.3)	8.0 (0.1)
Largemouth bass	6	4	12	73.0 (7.6)	20.3 (0.2)	8.1 (0.1)
Fathead minnow	7	4	36	50.9 (3.8)	20.5 (0.3)	8.1 (0.1)
Fathead minnow	8	4	32	51.1 (4.1)	20.8 (0.1)	7.8 (0.0)
Fathead minnow	9	4	28	50.7 (3.0)	21.0 (0.1)	7.6 (0.2)

(Vanderploeg and Scavia 1979; Lechowicz 1982). The E* index was calculated at the tank or treatment level, combining all diet data from fish in a given tank and the relative proportions of each of the 4 taxonomic zooplankton groups added to the tanks.

We tested the influence of DOC and changes in light climate on zooplanktivory and quantified the shape of that relationship using candidate model sets: (1) a null model that included only fish length and trial effects; (2) a linear model that added a linear light climate effect to the null model; and (3) a nonlinear model like the linear model except the influence of light was represented as a saturating function (Michaelis-Menton) or decreasing function (hyperbolic). Models were fit using maximum likelihood and the *optim* function in R (R Core Team 2013). We used a Poisson likelihood function for the largemouth bass and bluegill models because the response data (number of zooplankton in the diet) were counts, and a gamma likelihood function for minnows because the response variable (gut content weight) was continuous and positive. Model selection was based on Aikaike's information criteria (AIC). We tested for differences in tank conditions (temperature, dissolved oxygen, and fish length) using a 2-way ANOVA performed in the R statistical environment.

Results

Conditions of experimental tanks

DOC concentrations across feeding trial tanks ranged from 2.6 to 18.9 mg L^{-1}. The varied DOC concentrations had a strong influence on the average light climate within the tanks, which ranged from ~1 to 8 µmol m^{-2} s^{-1} (Fig. 1). There was a significant difference in water temperature in the tanks among trials for fathead minnow ($F_{2,5}$ = 12.29, p = 0.01) and bluegill ($F_{2,5}$ = 138.94, p < 0.001); however, this difference was due to time of day the experiments were conducted, and overall water temperature ranged from 19.3 to 23.0 °C. There was also a significant difference in water temperature among tanks for bluegill ($F_{4,5}$ = 65.23, p < 0.001), but temperatures only ranged from 21.8 to 23.0 °C. Similarly, there was a significant difference among trials in dissolved oxygen concentration in the tanks ($F_{2,3}$ = 12.05, p = 0.03; $F_{2,5}$ = 19.82, p = 0.004; $F_{2,4}$ = 299.00, p < 0.01 for largemouth bass, fathead minnow, and bluegill, respectively). The range in dissolved oxygen concentrations was low (6.37–8.95 mg L^{-1}) but not close to hypoxic conditions in any treatment. There was no significant difference in fish lengths among the tanks or trials for largemouth bass ($F_{2,27}$ = 0.81, p = 0.45 for trial effect; $F_{6,27}$ = 0.49, p = 0.81 for tank effect) or fathead minnow ($F_{2,89}$ = 0.091, p = 0.91 for trial effect;
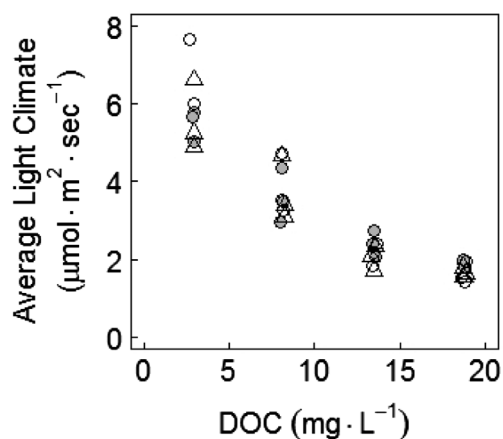

Figure 1. Influence of dissolved organic carbon (DOC) concentration on the average light climate in the experimental tanks. Open circles, open triangles, and filled circles represent experimental conditions from bluegill (*Lepomis macrochirus*), largemouth bass (*Micropterus salmoides*), and fathead minnow (*Pimephales promelas*) feeding trials, respectively. Light intensity across PAR (400–700 nm) was measured as the average in the tank to account for differences in ambient light over specific tanks. DOC was determined from measurements of water color following Lennon et al. (2013).

$F_{4,89}$ = 1.84, p = 0.12 for tank effect). There was a significant difference in bluegill total lengths among tanks ($F_{5,105}$ = 2.47, p = 0.04) but not among trials ($F_{2,105}$ = 1.77, p = 0.17). Bluegill lengths among trials ranged from 38 to 59 mm.

Effects of light climate on fish feeding rates and selectivity

DOC-induced differences in light climate affected feeding rates of all 3 fish species, despite the high individual variability in zooplankton consumed (Fig. 2, Table 2). Feeding rates were positively related to light climate for both bluegill and largemouth bass (Fig. 2a and b). Zooplanktivory rates were higher in bluegill than largemouth bass trials. A linear light effect provided the best description of the data for both of these species; there was no evidence to support a saturating light effect for bluegill and limited evidence to support a saturating light effect for largemouth bass (Table 2). Conversely, feeding rate was inversely related to light for fathead minnow and was best represented as a decreasing hyperbolic function of light (Fig. 2c, Table 2). In addition to the influence of light on fish feeding, we found that fish total length had a negative influence on both largemouth bass and bluegill zooplankton feeding rate, whereas we found no such influence for fathead minnow (Table 3).

Prey selection by bluegill and largemouth bass varied with prey size but was not strongly related to light. Bluegill
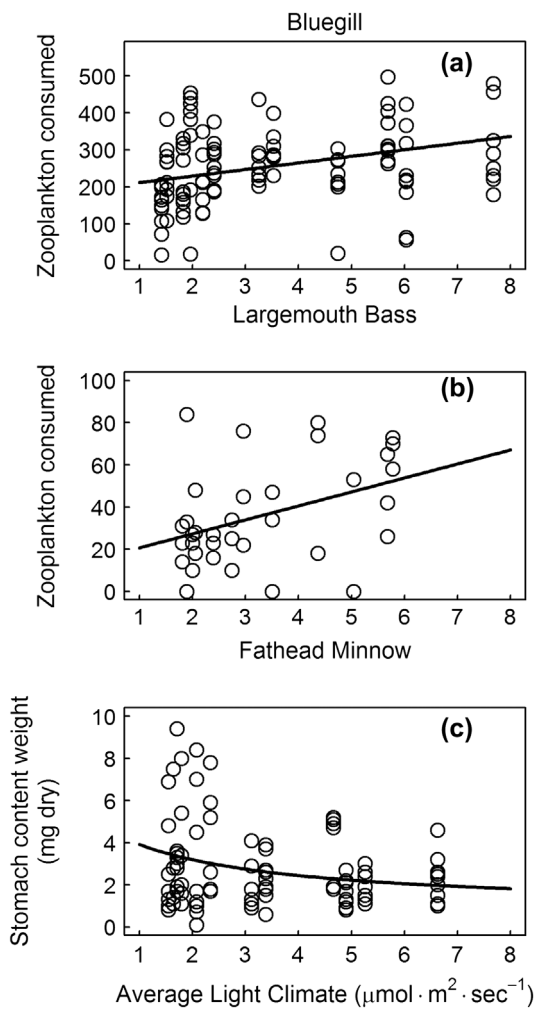
Figure 2. Average light climate, as modified by DOC, influenced zooplanktivory in laboratory feeding trials for 3 north temperate lake fishes. The best models suggested (a) bluegill and (b) largemouth bass zooplanktivory was positively and linearly associated with light, whereas the response in (c) fathead minnow was best represented by a decreasing, hyperbolic function of light. Minnow mastication prevented individual zooplankton enumeration; hence, gut contents were dried and weighed.

Table 2. Comparisons for 3 different models predicting the number of zooplankton consumed (bluegill and largemouth bass) or the gut content weight of zooplankton consumed (fathead minnow). All models include a linear term for fish length and categorical predictors representing trial and tank effects. The "light as linear" model includes a single coefficient representing the effect of average light climate on zooplankton consumed, whereas the "light as saturating" model uses a 2 parameter Michaelis-Menten function. The nonlinear model, "light as hyperbolic," represents the light effect on gut content weight using a 2 parameter hyperbolic function (i.e., $a/[b+\text{light}]$). The ΔAIC is the difference in the Akaike information criterion between the model and the best model for that species; RMSE is the square root of the mean squared error of the observations relative to the predictions.

Species	Model description	Parameters	Δ AIC	RMSE	$\sim R^2$
Bluegill	light as linear	5		900.0	0.28
Bluegill	light as saturating	6	11.9	903.6	0.26
Bluegill	no light	4	534.0	973.3	0.15
Largemouth bass	light as linear	5		124.0	0.22
Largemouth bass	light as saturating	6	3.1	124.0	0.22
Largemouth bass	no light	4	135.2	144.3	0.06
Fathead minnow	light as hyperbolic	6		17.3	0.13
Fathead minnow	light as linear	6	4.5	17.7	0.08
Fathead minnow	no light	5	108.7	96.8	0.08

Table 3. Parameter estimates and 95% confidence intervals for the best models predicting number of zooplankton consumed by bluegill and largemouth bass or gut content weight for fathead minnow.

Species	Model parameter	Parameter value	95% CI
Bluegill	intercept	473.7	(443.0, 504.4)
Bluegill	light	17.8	(16.28, 19.36)
Bluegill	fish length	−7.2	(−7.8, −6.55)
Bluegill	trial2	107.0	(99.61, 114.41)
Bluegill	trial3	49.9	(42.82, 57.06)
Largemouth bass	intercept	47.7	(29.53, 65.9)
Largemouth bass	light	6.6	(5.05, 8.21)
Largemouth bass	fish length	−0.5	(−0.68, −0.23)
Largemouth bass	trial2	−0.2	(−5.42, 5.02)
Largemouth bass	trial3	−2.5	(−7.18, 2.13)
Fathead minnow	light, hyperbolic a	10.17	(−13.46, 33.8)
Fathead minnow	light, hyperbolic b	2.29	(−3.99, 8.57)
Fathead minnow	fish length	0.01	(−0.03, 0.05)
Fathead minnow	trial2	0.35	(−0.01, 0.71)
Fathead minnow	trial3	1.29	(0.84, 1.74)

selectivity was slightly negative for small Cladocera and weak but positive for large Cladocera and *Chaoborus* (Fig. 3). Light climate did not influence bluegill selectivity within any of the zooplankton prey categories (all regression slopes: $p > 0.10$). For largemouth bass we found strong selection against small Cladocera and copepods and strong selection for Chaoboridae (Fig. 3). Largemouth bass selectivity for the large Cladocera was the only prey category in which selectivity was significantly related to light gradient ($p < 0.01$). The average proportion of zooplankton added that was consumed in the bluegill trials was 0.07, 0.08, 0.29, and 0.0 for small Cladocera, Copepoda, large Cladocera, and Chaoboridae, respectively. The average

proportion of zooplankton added that were consumed in the largemouth bass trials was 0.00, 0.10, 0.04, and 1.16 (ate more *Chaoborus* than we estimated were added based on tows) for small Cladocera, Copepoda, large Cladocera, and Chaoboridae, respectively.
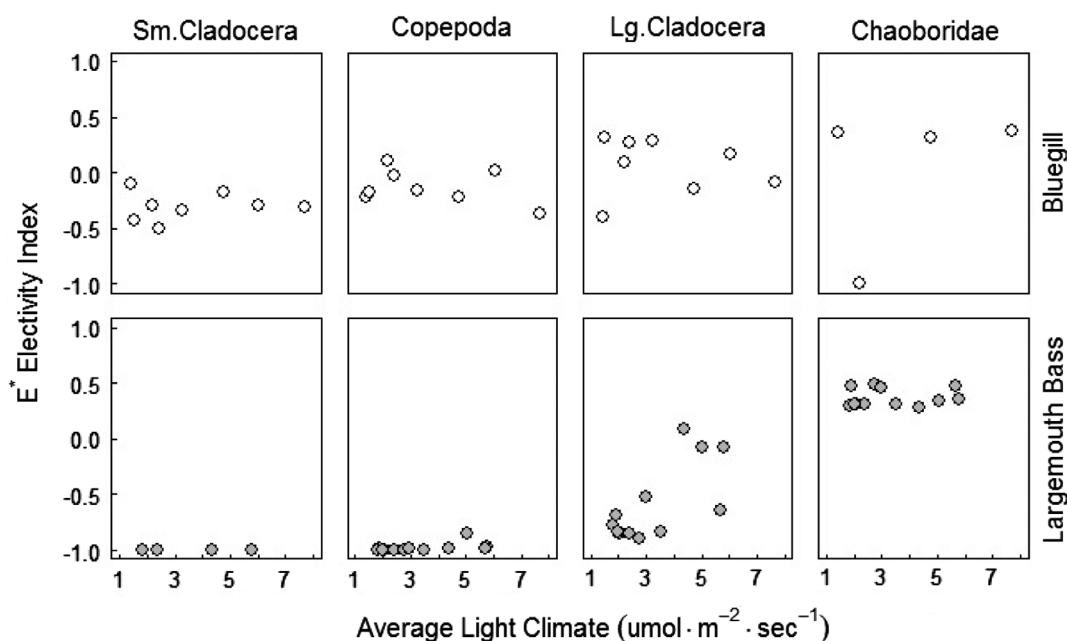
Figure 3. Electivity index of fish diet items relative to average experimental tank light climate for bluegill (top row, open circles) and largemouth bass (bottom row, filled circles). The feeding electivity index ranges from −1 to +1, where −1 represents avoidance or inaccessibility of the diet item and +1 indicates active selection (Vanderploeg and Scavia 1979; Lechowicz 1982).

Discussion

Although much of the fish feeding literature has focused on the role of turbidity in influencing zooplanktivorous feeding rates, recently published studies support our conclusions that higher DOC concentrations can influence fish feeding. Nurminen et al. (2014) found that a humic water treatment had a significant and negative effect on perch (*Perca fluviatilis*) feeding on *Chaoborus* sp. and that this effect was stronger than the influence of predation risk or interspecific competition. Although we found that higher DOC and lower light significantly reduced zooplankton feeding in largemouth bass and bluegill, as we hypothesized, our observed opposite influence of light for fathead minnows was unexpected.

Differences in predation risk across ontogeny may explain the contrasting effects of DOC on feeding rates between centrarchid largemouth bass and bluegill compared to cyprinid fathead minnows. As spined, deeper-bodied species, juvenile largemouth bass and bluegill maximize growth to reach a predation size refuge (Olson 1996; Post et al. 1998). By contrast, the ontogeny of the soft-rayed, shallow-bodied fathead minnow does not generally include a size-based predation refuge, and therefore this species and others like it may modify feeding behaviors in predation-prone environments, such as high-light environments, to reduce predation risk.

Anecdotally, fathead minnows in the high-light environments tended to exhibit more schooling behavior than bluegill or largemouth bass in similar high-light environments, a behavior linked to predator avoidance (Brock and Riffenburgh 1960) and reduced feeding rates (Eggers 1976). Although we did not specifically evaluate the effect of predators on zooplanktivory, the low light levels in our high DOC trials may have lowered the perceived predation risk of fathead minnows, resulting in our observed positive DOC–zooplanktivory relationship. Results of Ranåker et al. (2012) support the idea that DOC and light can influence prey fish behavior. They found the distance at which a prey fish attempted to escape from a predator was much shorter in humic water treatments relative to algae- and clay-treated water. Our results suggest fathead minnows may be less risk averse than centrachids in high DOC waters, resulting in the minnows exhibiting less predation avoidance behavior and feeding more in darker water.

The modest explanatory power of our models illustrated by the relatively low R^2 values (Table 2) indicates substantial variability in observed laboratory zooplanktivory that could not be accounted for by fish size, trial, or average light climate. Individual fish feeding on zooplankton in natural settings is highly variable, similar to our experimental observations. For instance, in a nearby study lake, similar-sized bluegill (mean total length = 49 mm) had on average 224 zooplankton in their gut (standard deviation = 636), but zooplankton counts across all individuals ranged from 0 to 4773 zooplanktoners (unpublished data). Similarly, individual variability in juvenile largemouth bass zooplanktivory in that lake was also highly variable (mean = 82 zooplanton per stomach,

standard deviation = 212, range = 0–1240; unpublished data). The mean and observed ranges of zooplanktivory from natural systems are consistent with our experimental observations. Despite the wide individual variability in feeding rates, AIC model selection criteria indicated models that included a term for light were far better supported than those that did not contain such a term (Table 2). Future studies evaluating factors that influence zooplanktivory should account for high variability in individual fish feeding rates when designing experiments.

In addition to the natural variability in feeding rates, other physiological differences among species may have led to significant variability in feeding rates. While bluegill and largemouth bass were obtained from the same lake as the source water for the experiments, fathead minnows were obtained from a bait shop with an unknown initial lake or pond source. As such, fathead minnows may have been pre-adapted to darker conditions than they experienced in the feeding trials. Limited evidence exists for foraging of light-adapted fish being more heavily influenced by changes in light availability compared to dark-adapted fish (Stasko et al. 2015). Physiological differences in spectral sensitivities for each species also may have led to a different response to changing light; however, we are unaware of any data on light adaptation or differences in spectral sensitivities for these specific species.

Prey type—more specifically zooplankton size and mobility—are also likely important factors influencing fish feeding under degraded optical conditions. Contrast degradation theory posits that for a given reduction in optical quality, there will be a greater negative effect on large items at distance than smaller, closer items (De Robertis et al. 2003). Our results found limited evidence to support this hypothesis. Although bluegill and largemouth bass trials showed stronger selectivity for the larger categories of zooplankton prey (large Cladocera, Chaoboridae) over the smaller classes (small Cladocera, Copepoda), the light climate did not generally influence selection, except where largemouth bass were slightly more selective for large Cladocera in darker environments (Fig. 3). Similarly, Jönsson et al. (2012) found the influence of humic water treatment on roach zooplanktivory was dependent on prey type where humic treatments reduced feeding on smaller copepod prey but did not influence the number of larger *Daphnia* consumed. This finding could also suggest that largemouth bass, bluegill, and fathead minnows will continue to feed optimally (Mittelbach 1983), regardless of light availability in the water column.

Prairie (2008) proposed that in many north temperate and boreal regions, DOC is as important as mineral nutrients in regulating lake ecosystems, yet our synthesis of the available literature suggests ecology has only recently recognized this role in fishes. For instance, Stasko et al. (2012) summarize the effects of "brownification" on lakes but reference a turbidity-focused study to illustrate how degraded visual environments influence fish feeding. Of the 7 papers we found that evaluated DOC or humic influences on fish feeding, all were in the last 5 years and primarily focused in northern Europe and species of that region. Our results suggest that common North American lake fishes are also likely influenced by DOC concentration and degraded visual environments. By using a range of DOC treatments in our experiment we were able to evaluate both the sign and potential shapes of the relationship between zooplanktivory and DOC. Our regression-based design, which contrasts with previous categorical approaches, enables better comparison to natural systems and the inclusion of our results in a predictive context (Cottingham et al. 2005).

Ecosystem-scale models are increasingly important tools for understanding the integrated effects of DOC on aquatic food webs via physical, chemical, and biological mechanisms. Concentrations of DOC are increasing in many parts of the world (Hongve et al. 2004; Monteith et al. 2007; Erlandsson et al. 2008), and it will be increasingly important for scientists and resource managers to use models to predict food web responses to this large-scale environmental change. For instance, Jones et al. (2012) used literature values to parameterize a lake model that explores how DOC concentration drives invertebrate consumer production. Experiments and parameterized model relationships that span likely DOC gradients, like those developed in this study, can extend such food web models to fishes. These models will generate new understanding and testable predictions about the impacts of changing DOC concentrations on lake food webs and fish populations.

References

Abrahams MV, Kattenfeld MG. 1997. The role of turbidity as a constraint on predator-prey interactions in aquatic environments. Behav Ecol Sociobiol. 40:169–174.

Ask J, Karlsson J, Persson L, Ask P, Byström P, Jansson M. 2009. Whole-lake estimates of carbon flux through algae and bacteria in benthic and pelagic habitats of clear-water lakes. Ecology. 90:1923–1932.

Brock VE, Riffenburgh RH. 1960. Fish schooling: a possible factor in reducing predation. ICES J Mar Sci. 25:307–317.

Cottingham KL, Lennon JT, Brown BL. 2005. Knowing when to draw the line: designing more informative ecological experiments. Front Ecol Environ. 3:145.

De Robertis A, Ryer CH, Veloza A, Brodeur RD. 2003. Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. Can J Fish Aquat Sci. 60:1517–1526.

Eggers DM. 1976. Theoretical effect of schooling by planktivorous fish predators on rate of prey consumption. J Fish Board Can. 33:1964–1971.

Erlandsson M, Buffam I, Fölster J, Laudon H, Temnerud J, Weyhenmeyer G, Bishop K. 2008. Thirty-five years of synchrony in the organic matter concentrations of Swedish rivers explained by variation in flow and sulphate. Glob Change Biol. 14:1191–1198.

Hambright KD, Hall BO. 1992. Differential zooplankton feeding behaviors, selectivities, and community impacts of two planktivorous fishes. Environ Biol Fish. 35:401–411.

Hanson PC, Carpenter SR, Cardille JA, Coe MT, Winslow LA. 2007. Small lakes dominate a random sample of regional lake characteristics. Freshwater Biol. 52:814–822.

Hongve D, Riise G, Kristiansen JF. 2004. Increased colour and organic acid concentrations in Norwegian forest lakes and drinking water – a result of increased precipitation? Aquat Sci. 66:231–238.

Jones SE, Solomon CT, Weidel BC. 2012. Subsidy or subtraction: how do terrestrial inputs influence consumer production in lakes? Freshwater Rev. 5:37–49.

Jönsson M, Ranåker L, Anders Nilsson P, Brönmark C. 2012. Prey-type-dependent foraging of young-of-the-year fish in turbid and humic environments: YOY fish foraging under visual constraints. Ecol Freshw Fish. 21:461–468.

Jönsson M, Ranåker L, Nilsson PA, Brönmark C, Grant J. 2013. Foraging efficiency and prey selectivity in a visual predator: differential effects of turbid and humic water. Can J Fish Aquat Sci. 70:1685–1690.

Karlsson J, Byström P, Ask J, Ask P, Persson L, Jansson M. 2009. Light limitation of nutrient-poor lake ecosystems. Nature. 460:506–509.

Kelly PT, Solomon CT, Weidel BC, Jones SE. 2014. Terrestrial carbon is a resource, but not a subsidy, for lake zooplankton. Ecology. 95:1236–1242.

Lechowicz MJ. 1982. The sampling characteristics of electivity indices. Oecologia. 52:22–30.

Lennon JT, Hamilton SK, Muscarella ME, Grandy AS, Wickings K, Jones SE. 2013. A source of terrestrial organic carbon to investigate the browning of aquatic ecosystems. PLOS ONE. 8(10):e75771.

Mittelbach GG. 1983. Optimal foraging and growth in bluegills. Oecologia. 59:157–162.

Monteith DT, Stoddard JL, Evans CD, de Wit HA, Forsius M, Høgåsen T, Wilander A, Skjelkvåle BL, Jeffries DS, Vuorenmaa J, et al. 2007. Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. Nature. 450:537–540.

Morris DP, Zagarese H, Williamson CE, Balseiro EG, Hargreaves BR, Modenutti B, Moeller R, Queimalinos C. 1995. The attenuation of solar UV radiation in lakes and the role of dissolved organic carbon. Limnol Oceanogr. 40:1381–1391.

Nurminen L, Estlander S, Olin M, Lehtonen H. 2014. Feeding efficiency of planktivores under disturbance, the effect of water colour, predation threat and shoal composition: feeding of planktivores under disturbance. J Fish Biol. 84:1195–1201.

Olson MH. 1996. Predator-prey interactions in size-structured fish communities: implications of prey growth. Oecologia. 108:757–763.

Post DM, Kitchell JF, Hodgson JR. 1998. Interactions among adult demography, spawning date, growth rate, predation, overwinter mortality, and the recruitment of largemouth bass in a northern lake. Can J Fish Aquat Sci. 55:2588–2600.

Prairie YT. 2008. Carbocentric limnology: looking back, looking forward. Can J Fish Aquat Sci. 65:543–548.

R Core Team. 2013. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.

Ranåker L, Jönsson M, Nilsson PA, Brönmark C. 2012. Effects of brown and turbid water on piscivore-prey fish interactions along a visibility gradient: predator-prey interactions in reduced visibility. Freshwater Biol. 57:1761–1768.

Roulet N, Moore TR. 2006. Environmental chemistry: browning the waters. Nature. 444:283–284.

Solomon CT, Jones SE, Weidel BC, Buffam I, Fork ML, Karlsson J, Larsen S, Lennon JT, Read JS, Sadro S, Saros JE. 2015. Ecosystem consequences of changing inputs of terrestrial dissolved organic matter to lakes: current knowledge and future challenges. Ecosystems. 18:376–389.

Stasko AD, Gunn JM, Johnston TA. 2012. Role of ambient light in structuring north-temperate fish communities: potential effects of increasing dissolved organic carbon concentration with a changing climate. Environ Rev. 20:173–190.

Stasko AD, Johnston TA, Gunn JM. 2015. Effects of water clarity and other environmental factors on trophic niches of two sympatric piscivores. Freshwater Biol. 60:1459–1474.

Tranvik LJ. 1990. Bacterioplankton growth on fractions of dissolved organic carbon of different molecular weights from humic and clear waters. Appl Environ Microbiol. 56:1672–1677.

Utne-Palm AC. 2002. Visual feeding of fish in a turbid environment: physical and behavioural aspects. Mar Freshw Behav Physiol. 35:111–128.

Vanderploeg HA, Scavia D. 1979. Two electivity indices for feeding with special reference to zooplankton grazing. J Fish Board Can. 36:362–365.

Vinyard GL, O'Brien WJ. 1976. Effects of light and turbidity on the reactive distance of bluegill (*Lepomis macrochirus*). J Fish Board Can. 33:2845–2849.

Wilkinson GM, Pace ML, Cole JJ. 2013. Terrestrial dominance of organic matter in north temperate lakes. Glob Biogeochem Cy. 27:43–51.