

Dissolved Organic Carbon and the Foraging and Prey Selection of Largemouth Bass

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Abstract

Dissolved organic carbon (DOC) is a major factor determining the physical and biological structure of freshwater systems. DOC levels in lakes of North America and Europe have risen over the past two decades, thus research into the effects of high DOC on aquatic communities is timely and necessary. One potential result of DOC input and lake darkening is a reduction in productivity across multiple trophic levels, including primary producers, benthic invertebrates, pelagic organisms, and fish. In addition to reducing productivity, light limitation associated with DOC may lead to changes in animal behavior. In this study, I investigated the effect of DOC on foraging and prey preference of a visual predator, the largemouth bass (*Micropterus salmoides*), in a whole-lake experiment. Gastric lavage and diet analysis of bass on East Long Lake (high DOC) and West Long Lake (low DOC) were conducted to test the hypothesis that foraging success, indicated by total biomass of stomach contents, would be lower under high DOC conditions. Furthermore, I predicted bass in the darker water would reduce consumption of pelagic prey and increase consumption of benthic prey by switching from visual to tactile foraging methods. Results showed that the biomass of stomach contents was the same in East and West Long, and the proportion of benthic and terrestrial prey in bass diets was similar. In contrast to my hypothesis, bass in the high-DOC lake consumed significantly more pelagic prey. One possible explanation is that productivity responds unimodally to DOC, so that lakes with moderately-high DOC levels are highly productive, while very dark, high-DOC lakes are light-limited and less productive. Data suggests East Long has higher pelagic productivity at current DOC levels (~12 mg/L) than West Long (~6mg/L), and this is reflected in the greater importance of pelagic prey in East Long bass diets.

Introduction

Dissolved organic carbon (DOC), consisting of material derived from the breakdown of terrestrial plant matter, can affect a variety of physical characteristics of lakes, and thus plays a major role in structuring the composition of aquatic communities. In the past two decades, a trend of rising DOC in lakes across North America and Europe has been observed (Monteith et al. 2007). Both climate change and changes in land use can alter input of terrestrial carbon to lakes, and have the potential to significantly alter aquatic ecosystems (Houser 2006). In a study of small, north-temperate lakes, Houser (2006) found that lakes with high DOC are darker in color, with decreased depth of the light penetration, a shallower, colder epilimnion, and reduced mean epilimnetic irradiance. Furthermore, DOC may act to buffer small lakes from a changing climate by absorbing radiation and moderating water temperature (Read and Rose 2013).

DOC has been shown to limit lake productivity, including primary and zooplankton production in the epilimnetic zone (Kelly et al. 2014). Changes in primary production related to DOC may in turn affect the abundance of organisms at higher trophic levels; for example, light limitation in oligotrophic, highly colored lakes has been correlated with lower productivity of benthic invertebrates and fish (Karlsson et al. 2009, Craig et al. in review). These studies indicate high DOC may result in decreased abundance of prey available for predatory fish and reduced productivity at multiple trophic levels.

In addition to its effect on productivity and community structure, water color may also influence the foraging success of fish that rely on visual predation. Previous studies on piscivorous fish found the number of prey captured and consumed decreased significantly as water turbidity increased, due to increased light attenuation and reduced visibility of prey (De Robertis et al. 2003). One might expect to observe a similar decline in fish foraging success in

high DOC lakes, as both turbid and humic (high-DOC) water reduce visual clarity. However, turbidity and DOC differ in the way they degrade optical conditions in the lake, in that turbidity scatters light, while DOC absorbs light (Jonsson et al. 2013). Jonsson et al. (2013) compared the effects of turbidity and high DOC on a visual predator, the northern pike, and found the rate of prey encounter of northern pike decreased in both turbid and humic water. Interestingly, the rate of successful prey capture was high in clear and highly humic water but low in moderately humic water; Jonsson et al. attributed this pattern to the decreased ability of prey to detect an approaching predator in very low light conditions. Similar unimodal patterns in productivity have been described for fish and zooplankton (Finstad et al. 2014, Kelly et al. 2014), both of which are preyed on by largemouth bass. This suggests the effects of DOC on fish foraging may be nonlinear and depend on the relative concentration of colored organic material.

In this study, I investigated the effect of DOC on foraging success and prey preference of largemouth bass (*Micropterus salmoides*) in a whole-lake experiment. Largemouth bass prey on a variety of pelagic, benthic and terrestrial organisms including zooplankton, gastropods, chironomids, odonates, aquatic insect larvae, terrestrial invertebrates, juvenile bass and other fish, and small terrestrial vertebrates (Hodgson and Kitchell 1987). Because they consume a wide variety of species from multiple habitats and trophic levels, and because they rely primarily on visual cues when hunting (Nyberg 1971), largemouth bass are ideal model organisms to investigate the effect of water color on prey selection by a top predator. I analyzed the diet of largemouth bass in East Long Lake (high DOC) and West Long Lake (low DOC) in order to test the following hypotheses: 1) the biomass of total stomach contents per fish (relative to fish body weight) will be lower in East Long than West Long, because high DOC and darker water in the east basin will make it harder for bass to find and capture prey, resulting in lower overall

foraging success; 2) bass will selectively forage for benthic prey and consume proportionally fewer pelagic prey in East Long compared to West Long, because they will rely more on tactile foraging methods and less on visual predation in the darker water. One aim of this study is to determine whether a reduction in food intake, caused by lower bass foraging success in high-DOC water, is a mechanism for the decline in fish productivity observed by Karlsson et al. (2009). The whole lake manipulation is an ideal experimental setup because it allows for observations of the effects of increased DOC while keeping other variables within the lake constant, mimicking temporal changes across a spatial divide (Craig, personal communication).

Methods

This study was conducted on Long Lake, an 8.9 hectare lake located at the University of Notre Dame Environmental Research Center, located on the Upper Peninsula in Gogebic County, Michigan. In September 2012, the lake was divided into east and west basins using an impermeable plastic curtain (Craig, N. personal communication). East Long receives a larger input of terrestrial organic matter, resulting in high DOC and brown colored water, while West Long serves as a control with low DOC.

Bass were obtained by angling in the east and west basins of Long Lake from May through July 2014 during morning and afternoon sampling sessions. Data were collected from 83 bass in East Long and 94 bass in West Long. Length and mass measurements of each fish were taken, and the stomach contents were obtained by gastric lavage and preserved in 70% ethanol. For the diet analysis, I measured the body length or head width of each prey item and calculated its dry weight based on published equations (Appendix 1). When the body was absent in the diet and dry mass could not be calculated directly from head width, I estimated body

length based on comparison to prey items with similar dimensions. Each prey item was identified to the lowest possible taxon (order or family), and classified by habitat type. Amphipods, hydrachnidae (water mites), hemiptera, hirudinea (leeches), and oligochaetes were classified as benthic, along with aquatic larval insects such as chironomids, sialidae, trichoptera, lepidoptera, anisoptera, zygoptera, and ephemeroptera naiads. Pelagic prey consisted of frogs (amphibia), minnows of largemouth bass or other fish, chaoborus larvae and pupae, cladocerans, chironomid pupae, and nepidae (water scorpions). Among the terrestrial prey items were arachnids, adult diptera, hymenoptera (ants), adult odonates, adult trichoptera, other winged terrestrial invertebrates, and one salamander.

To analyze the data, I calculated the mean dry biomass of total stomach contents per fish in East and West Long. A t-test was used to compare biomass of stomach contents, relative to fish body weight, between East and West Long. Furthermore, I compared the importance of benthic, pelagic and terrestrial prey items in high and low DOC conditions by calculating the proportion of each prey category out of total stomach contents (by dry weight). A t-test was used to compare the proportion of each prey class in East and West Long. The dry mass method was chosen in this study since it provides a better estimate of the energetic contribution of a prey type than numeric abundance (Hyslop 1980).

Results

Diet patterns and prey preference were largely similar among largemouth bass in the high and low-DOC lakes. Although bass in West Long tended to eat more, relative to body weight, than bass in East Long, the difference in total mass of stomach contents was not significant (Figure 1). I found that pelagic prey made up a significantly larger proportion of the diets in East Long (34.6%) compared to West Long (20.9%) ($p=0.027$, $t=2.24$, $df=167$). West Long bass

consumed a slightly larger proportion of terrestrial prey than East Long Bass, but the difference was not significant, and the proportion of benthic prey in the diets was similar between east and west basins (Table 1, Figures 2 & 3).

Analysis at the level of prey orders yielded further support for these results. The most abundant pelagic prey items were chaoborus larvae, cladocerans, and fish, and these items were found in 43%, 9.6%, and 19% of the diets from West Long Lake, respectively, compared to 21%, 1.1%, and 8.5% of diets from East Long. Among terrestrial prey, odonate adults were very abundant in diets from both lakes. Although East and West Long did not differ significantly in the proportion of terrestrial prey in bass diets, the mass of odonate adults consumed was greater in West Long, with an average of 1.22 ± 3.74 mg odonates per gram bass, compared to 0.48 ± 1.26 mg per gram bass in East Long ($p=0.072$, $t=-1.82$, $df=116$).

Discussion

Data from the diet analysis was used to evaluate two hypotheses: that total mass of stomach contents would be lower under high-DOC conditions in East Long compared to West Long, and bass would decrease consumption of pelagic prey and increase consumption of benthic prey in East Long. I found little support for my original hypotheses under the current experimental conditions. Total biomass of stomach contents per fish was greater in West Long than East Long; however, the difference was not significant. Furthermore, I found the proportion of pelagic prey in bass diets was significantly greater in East Long, where DOC is higher and the water is darker. This is in contrast to my hypothesis that low light conditions would impair visual foraging ability of largemouth bass and reduce pelagic consumption in the high-DOC lake.

I predicted the biomass of stomach contents per fish would be lower in East Long than West Long, and this could occur for two reasons: foraging is more difficult in highly humic water due to low light conditions, as demonstrated by Jonsson et al. (2013); and/or the availability of prey is lower due to reduced overall productivity in high-DOC lakes. Under the first scenario, bass would be expected to adapt to high-DOC, low light conditions in East Long by switching from a heavy reliance on visual predation to more tactile foraging behavior, resulting in consumption of fewer pelagic prey in East Long than West Long and more benthic prey. This was not observed in the current study. The hypotheses tested in this study were based on the assumption that bass are limited in prey selection by their ability to locate and capture prey in highly colored water. However, this may not be the case if poor visual quality is offset by other factors, such as increased prey abundance.

Although numerous studies have linked increasing DOC with declines in lake primary and secondary productivity (Karlsson et al. 2009, Kelly et al. 2014, Craig et al. in review), recent findings suggest the net effect of DOC may involve a tradeoff between positive and negative factors. Finstad et al. (2014) described a unimodal response of brown trout across a gradient of DOC concentrations in boreal, oligotrophic lakes. Trout biomass was lowest at low (<1mg/L) and high (~7mg/L) levels of DOC, and trout productivity was highest at intermediate levels of DOC. It has been suggested that DOC input initially promotes lake productivity via energy and nutrient subsidies and by screening harmful UV radiation (Finstad et al. 2014). As DOC levels continue to rise, the amount of light available for photosynthesis becomes limiting and productivity begins to decline.

A similar unimodal response was observed in studies of zooplankton secondary production in northern temperate lakes. Kelly et al. (2014) measured the density of cladocera

larvae, a major prey item of largemouth bass, and found cladocera density was variable, reaching densities up to 1000 individuals per square meter in lakes with low to moderate DOC, but declined drastically in lakes with the highest DOC concentrations (~17-22mg/L). The current DOC level in East Long is approximately 12mg/L, while West Long has decreased to ~6mg/L DOC (Craig, N., personal communication). By comparison to lakes in previous studies, East Long is only moderately high in DOC and brown coloration; this suggests East Long has not yet reached a threshold DOC level, where the water is so dark that lake productivity begins to decline. If this is the case, then slightly elevated levels of DOC in East Long might currently enhance productivity of zooplankton and invertebrates compared to West Long; thus, increased abundance of prey in East Long might offset the reduction in fish prey capture in darker, high-DOC water described by Jonsson et al. (2013).

According to a functional response model, prey should appear in the diet of a predator in proportion to their abundance or encounter frequency (Hodgson and Kitchell 1987); as a generalist predator in lake ecosystems, bass diets can serve as indicators of benthic and pelagic invertebrate communities in lakes. I observed an increased proportion of pelagic prey in diets of East Long bass compared to West Long, reflecting an increase in pelagic productivity under moderately high DOC levels of ~12mg/L. Further analysis showed the majority of pelagic prey in bass diets consisted of chaoborus larvae, cladocerans, small fish, and a few large frogs. These items were found more frequently in the diets of East Long bass than West Long bass. For example, chaoborus larvae were found in 43% of East Long diets, while only 21% of West Long diets contained chaoborus. Similar trends were observed for cladocerans and fish, which appeared in 9.6% and 19% of East Long diets, respectively, but only 1.1% and 8.5% of West Long diets. Under a functional response model, the greater frequency of these organisms in bass

diets of East Long suggests productivity is higher in East than West Long at current DOC levels. However, as DOC continues to rise in East Long, productivity is expected to decline and pelagic prey will become harder to catch and less important in the diets of East Long bass. This may occur after the lake crosses its threshold DOC value, where the negative effects of DOC outweigh the positive effects.

Overall, the results of this study do not support a foraging limitation hypothesis to explain the reduction in fish productivity observed by Karlsson et al. (2009) in high-DOC lakes. The rate of prey capture and consumption, indicated by total biomass of stomach contents, did not decline under current moderately high levels of DOC in East Long. Nevertheless, changes in DOC can impact freshwater communities in multiple ways, including resource availability and habitat limitation. For example, Craig et al. (in review) showed that high DOC concentrations limited zoobenthos production by decreasing the availability of dissolved oxygen in darker, colder lakes. These benthic organisms constitute an important food resource for largemouth bass. Reduced zooplankton productivity observed in humic waters may limit the growth of planktivorous fish populations (Kelly et al. 2014). In addition to suffering from resource depletion, fish may be subject to a “habitat squeeze” as the warm, oxygen-rich epilimnion layer becomes narrower in dark, high-DOC lakes. Thus, widespread changes in DOC input to lake ecosystems (Monteith et al. 2007) have the potential to drastically alter economically and recreationally important fish communities. As this study showed, the effects of DOC on aquatic ecosystems can be varied, and different lakes may have different threshold DOC levels where major negative effects become apparent. In the context of continual changes in land use, climate, and DOC, the study of lake food webs in relation to carbon input is extremely important.

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Table 1. Proportions of benthic, pelagic, and terrestrial prey in the diets of largemouth bass, by dry weight. Values indicate the average proportion of each prey type in East (high DOC) and West Long (low DOC) \pm standard deviation.

		East Long	West Long
Sample size		83	94
Total diet mass relative to fish body weight		1.94 \pm 5.48	2.52 \pm 6.29
Proportion of prey habitat type in diets	Benthic	0.24 \pm 0.37	0.21 \pm 0.37
	Pelagic	0.35 \pm 0.43	0.21 \pm 0.39
	Terrestrial	0.30 \pm 0.42	0.40 \pm 0.47
	Unknown	0.0001 \pm 0.0006	0.02 \pm 0.15

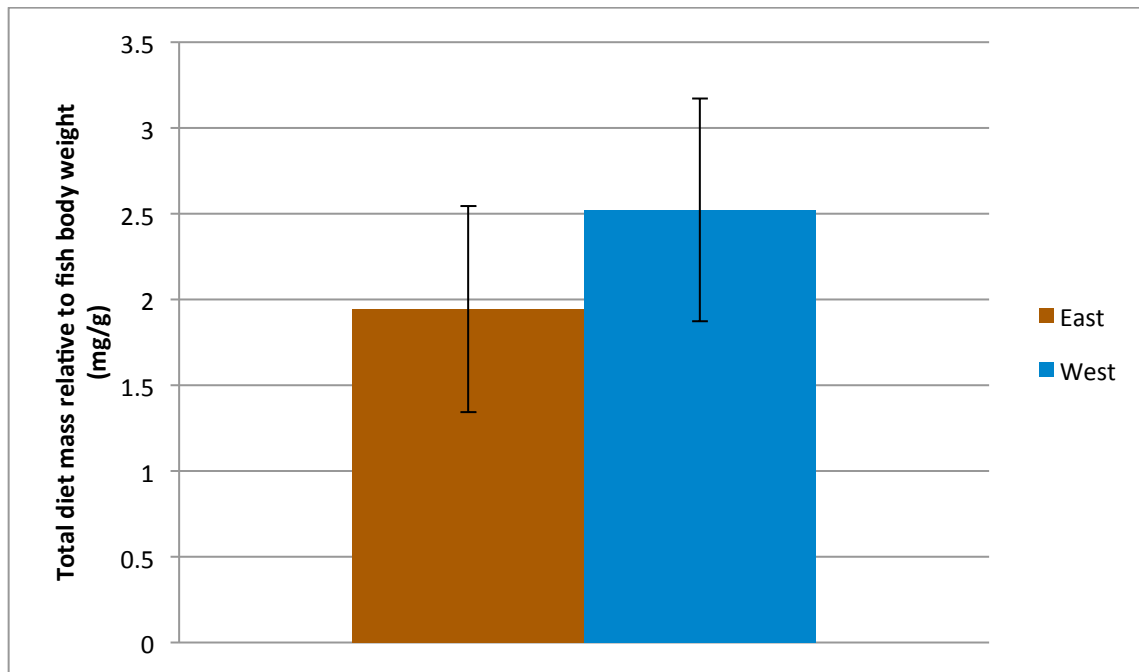


Figure 1. Total dry mass of stomach contents relative to fish body weight in East Long (high DOC) and West Long (low DOC). There was no significant difference in total stomach contents, indicating that foraging success did not differ between the lakes. Error bars indicate standard error.

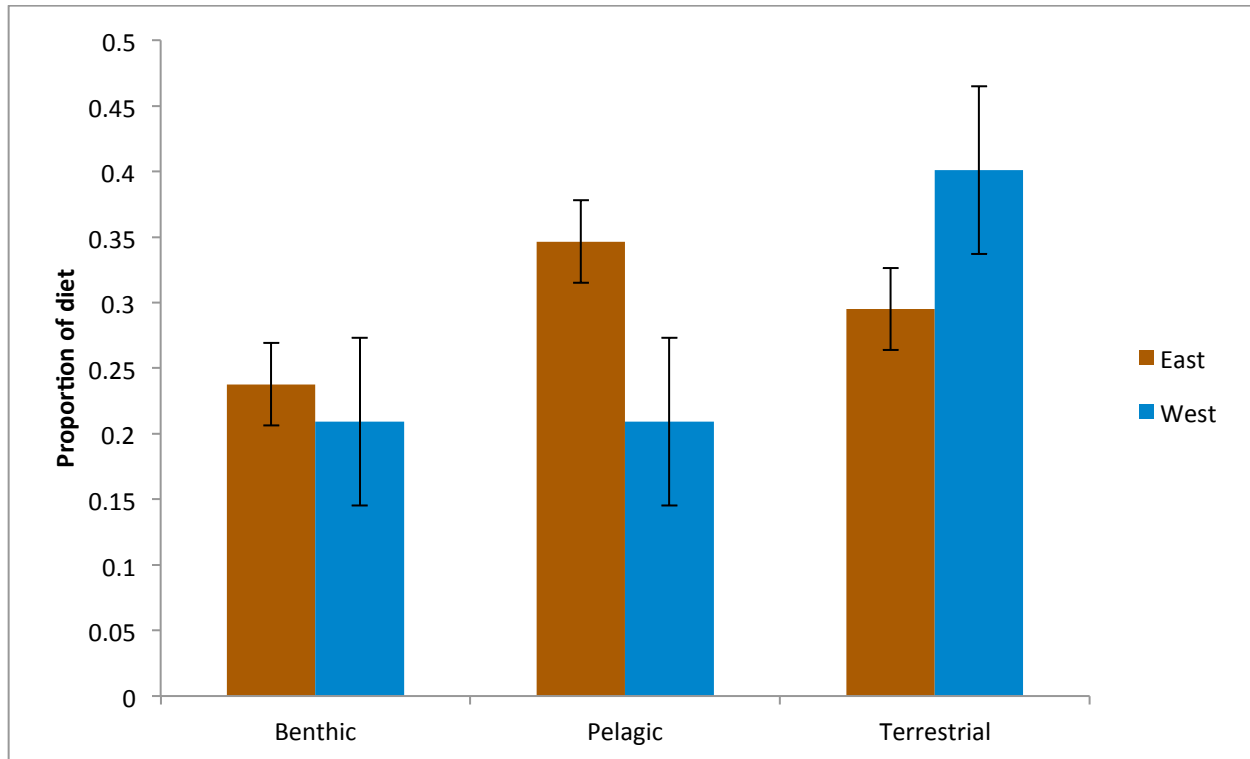


Figure 2. Proportion of bass diet consisting of benthic, pelagic, and terrestrial prey by dry weight in East Long (high DOC) and West Long (low DOC). Prey preference was similar between the two lakes, although the proportion of pelagic prey in bass diets was significantly greater in East Long than West Long ($p=0.027$, $t=2.24$, $df=167$). Error bars indicate standard error.

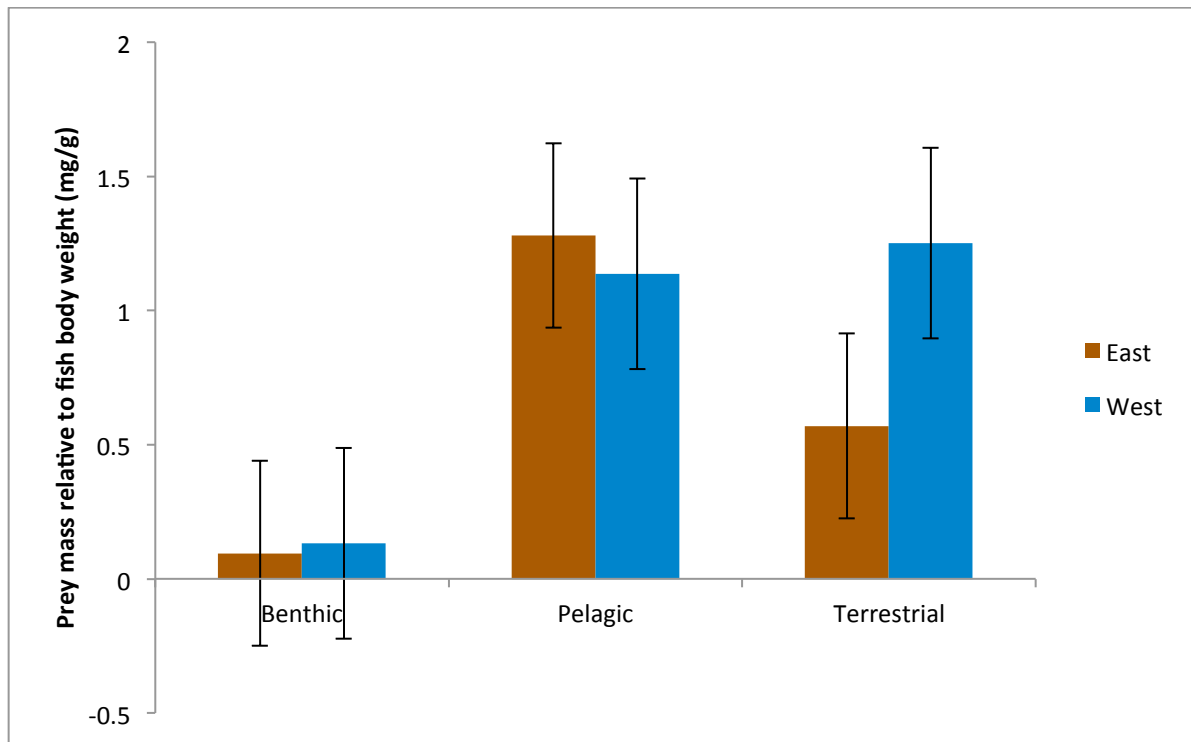


Figure 3. Dry mass of benthic, pelagic, and terrestrial prey in bass diets, relative to fish body weight. Dry mass of each prey category was used to calculate the proportion of that prey category in the total bass diet. Error bars indicate standard error.

Appendix 1. Length-mass regression equations used to calculate dry mass of prey items.

DM=dry mass (mg), L=body length (mm).

Prey Item	Equation	Reference
Amphibian	*Dry mass measured directly	
Amphipoda	$DM=0.002*L^{3.211}$	Benke et al (1999)
Anisoptera naiad	$DM=0.0076*L^{2.809}$	Benke et al (1999)
Arachnid	$Ln(DM)=-7.849+0.49335*L+0.0080448*L^2$	Sage (1982)
Benthic invertebrate unidentifiable	$DM=0.0018*L^{2.617}$	Benke et al (1999)
Benthic invertebrate unidentifiable larvae	$DM=0.0018*L^{2.617}$	Benke et al (1999)
Benthic invertebrate unidentifiable pupae	$DM=0.0018*L^{2.617}$	Benke et al (1999)
Ceratopogonidae larvae	$DM=0.00022*L^{2.871}$	Benke et al (1999)
Chaoborus larvae	$DM=0.001425*L^{3.599}$	Ramcharan et al (2001)
Chaoborus pupae	$DM=0.001425*L^{3.599}$	Ramcharan et al (2001)
Chironomidae larvae	$DM=0.0018*L^{2.617}$	Benke et al (1999)
Chironomidae pupae	$DM=0.004571*L^{2.53}$	Methot et al (2012)
Cladocera	$DM=0.011705*L^{2.52}$	McCauley (1984)
Coleoptera aquatic	$DM=0.0077*L^{2.91}$	Benke et al (1999)
Diptera	$DM=0.0025*L^{2.692}$	Benke et al (1999)
Diptera adult	$Ln(DM)=-9.314+0.66297*L-0.016486*L^2$	Sage (1982)
Diptera larvae	$DM=0.0025*L^{2.692}$	Benke et al (1999)
Ephemeroptera naiad	$DM=0.0025*L^{2.692}$	Benke et al (1999)

Ephemeroptera_pupae	$DM=0.0025*L^{2.692}$	Benke et al (1999)
Fish_unidentifiable	$DM=0.02118*L^{2.3473}$	Nikki Craig – unpublished data
Hemiptera	$DM=0.0108*L^{2.734}$	Benke et al (1999)
Hirudinea	$DM=0.04076*L^{2.22}$	Edwards et al (2009)
Hydrachnidae	$DM=0.13265*L^{1.66}$	Baumgartner & Rothaupt (2003)
Hymenoptera_adult	$DM=0.01379*L^{2.696}$	Bradley et al (1993)
Invertebrate_unidentifiable	$\ln(DM) = -7.761 + 0.34975*L + 0.0039315*L^2$	Sage (1982)
Largemouth_bass	$DM=0.02118*L^{2.3473}$	Nikki Craig – unpublished data
Lepidoptera_larvae	$DM=0.0027*L^{2.918}$	Benke et al (1999)
Megaloptera_larvae	$DM=0.0031*L^{2.801}$	Benke et al (1999)
Nepidae	$DM=0.02*L^{2.981}$	Miyasaka et al (2008)
Odonata_adult	$DM=0.14*L^{2.27}$	Sabo et al (2002)
Odonata_naiad	$DM=0.0076*L^{2.809}$	Benke et al (1999)
Oligochaeta	$DM=0.005888*L^{1.54}$	Methot et al (2012)
Plecoptera_adult	$DM=0.0128*L^{2.539}$	Bradley et al (1993)
Plecoptera_naiad	$DM=0.0094*L^{2.754}$	Benke et al (1999)
Salamander	*Dry mass measured directly	
Sialidae_adult	$\ln(DM) = -7.761 + 0.34975*L + 0.0039315*L^2$	Sage (1982)
Sialidae_larvae	$DM=0.0031*L^{2.801}$	Benke et al (1999)

Slug	$DM=0.04076*L^{2.22}$	Edwards et al (2009)
Terrestrial_invertebrate	$Ln(DM)=-7.761+$ $0.34975*L+0.0039315*L^2$	Sage (1982)
Terrestrial_orthoptera	$Ln(DM)=-7.036+0.27651*L -$ $0.0027946*L^2$	Sage (1982)
Trichoptera_adult	$DM=0.00995*L^{3.044}$	Bradley et al (1993)
Trichoptera_nymph	$DM=0.0056*L^{2.839}$	Benke et al (1999)
Trichoptera_pupae	$DM=0.0056*L^{2.839}$	Benke et al (1999)
Unidentifiable	$Ln(DM)=-7.761+$ $0.34975*L+0.0039315*L^2$	Sage (1982)
Yellow perch	$DM=0.02118*L^{2.3473}$	Nikki Craig – unpublished data
Zygoptera_adult	$DM=0.14*L^{2.27}$	Sabo et al (2002)
Zygoptera_naiad	$DM=0.0051*L^{2.785}$	Benke et al (1999)

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