

Feeding habits of yellow perch *Perca flavescens* and bluegill *Lepomis macrochirus* in clear and  
humic lakes

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Caitlin Broderick

Advisor: Nicola Craig 2015

## **Abstract**

Climate and land use change contribute to increasing dissolved organic carbon (DOC) in lakes in Europe and North America, necessitating research on lake physical properties, primary productivity and faunal communities. Darker water caused by DOC reduces depth of primary production, limit dissolved oxygen in deep water, and inhibit visual predation of planktivorous fish. This study investigates the effects of DOC concentration on the diets of juvenile bluegill and yellow perch, two species with developmental transitions from planktivory to benthic feeding, from clear and dark lakes. We hypothesized that fish stomach contents in a dark lake would show a higher benthic proportion of prey items. We also hypothesized that the proportion of benthic prey items would increase with size, and that the increase would be faster relative to size in darker lakes. Gastric lavage and analysis of stomach contents by dry weight were used to quantify benthic, pelagic and terrestrial prey items relative to fish size. Our study showed that the stomachs of fish from a dark lake were significantly fuller than those of fish from a light lake, and that the difference came primarily from increased pelagic feeding in dark-lake bluegill. In Crampton Lake, pelagic feeding was also shown to increase with body length in bluegill and decrease with body length. No significant relationship between body length and diet composition was found in either species in Hummingbird Lake. These results suggest that other factors, such as improved habitat for small zooplankton in humic lakes, counteracted light limitations on visual hunting.

## **Introduction**

Dissolved organic carbon (DOC) in aquatic ecosystems refers to any organic compounds in water able to pass through a filter (.45 micrometer standard; Ogawa and Ogura 1992). Generally, DOC makes up half of all dissolved organic matter (Tipping 1999), which is supplied to lakes through terrestrial input and through primary production (Bertilsson and Tranvik 2000).

Lakes with high DOC concentration are referred to as humic lakes and develop a characteristic brown color. DOC is an important part of the carbon cycle in freshwater lakes and helps determine physical properties such as thermal and epilimnetic structure in small lakes due to reduced light and heat penetration (Read and Rose 2013).

DOC levels have been increasing in freshwater lakes over the past few decades. This trend corresponds to rising temperatures, which causes phenol oxidase, an enzyme necessary to break down organic material in ecosystems, to become overactive (Freeman et al. 2001, Shi 2011). Many regional variables such as solar radiation and precipitation have been shown to affect DOC concentrations (Zhang et al. 2010), and climate-related changes may cause more pronounced DOC effects. Optimistic aquatic ecologists consider DOC increases to be consistent with the reduction of anthropogenic sulfur deposition in lakes: organic compounds buffer pH change due to sulfate, and the current spike is due to the lag in DOC concentration adjustment (Monteith et al. 2006). Lake darkening, whether by natural or human-influenced processes, causes significant changes in physical properties and therefore the life it can support.

Flora and fauna receive less sunlight in humic lakes, which can have a variety of effects on aquatic biota. Lake browning increases UV-light attenuation (Morris et al. 1995), protecting organisms from toxic radical compounds while limiting the depth at which photosynthesis can occur (Schindler et al. 1996). By decreasing the depth of the photic zone, high levels of humic substances cause hypolimnion hypoxia and can significantly affect lake structure and aquatic communities (Taipale et al. 2009; Nürnberg 2004). However, though phytoplankton range is reduced in humic lakes, high allochthonous carbon inputs provide a low-quality but abundant resource for zooplankton (Brett et al. 2009). Humic substances have been shown to sustain high populations of bacteria on which zooplankton feed (Jones 1992), while some zooplankton are

adapted to utilize allochthonous DOC directly (Hessen et al. 1990). The multifold effects of DOC on lake structure have resulted in several models for humic lake productivity. One study suggests that high DOC limits productivity of organisms throughout the food web, including benthic invertebrates and fish (Karlsson et al. 2009). Other studies suggest unimodal relationships between DOC and fish production, indicating that DOC has several effects that create a threshold between positive and negative effects (Finstad et al. 2014).

In addition to determining food availability for freshwater fish, lake browning can also affect fish foraging by limiting visibility. For fish reliant on sight for foraging, less light availability makes it difficult to detect and consume prey (Vinyard and O'Brien 1976). Studies show that the ability to search for and locate prey is critical to zooplanktivory (O'Brien 1979). Additionally, though size-selection of benthic items like chironomids may be impaired by low-light conditions, benthic feeding is largely independent of visual cues (Rowe et al. 2003). Omnivorous fish play an important role in combining the benthic and pelagic food webs by combining light-dependent and light-independent foraging methods (Wagner et al. 2012). Low-light conditions due to high DOC may cause a diet shift towards benthic prey.

Yellow perch *Perca flavescens* and bluegill *Lepomis macrochirus* are found throughout North American freshwater lakes and show dietary transitions during development. Juveniles of both species switch from feeding on zooplankton to feeding on benthic invertebrates before switching to a diet of small fish and open-water zooplankton (Allen 1935; Michigan DNR 2015). Yellow perch and bluegill are also vision-oriented selective predators (Jakobsen and Johnsen 1987). Research suggests that water color affects prey selection by yellow perch; in clearer water, perch feed on large-sized cladocera, a pelagic prey item (Estlander et al. 2010). But yellow perch have been shown to tolerate low-oxygen conditions in humic lakes, and they will to

continue to forage for benthic prey items in these environments (Roberts et al. 2012). This would suggest that humic waters would make pelagic feeding less efficient but have little effect on benthic feeding. In yellow perch and bluegill, it could be favorable to switch to benthic foraging earlier in development to compensate for visual limitations to planktivory.

This study aimed to investigate the effects of DOC concentration on the diets of juvenile bluegill and yellow perch from a clear-watered lake and a dark-watered lake. We hypothesized that benthic items will compose a larger part of fish diet in the dark lake to compensate for reduced visibility for pelagic hunting. Additionally, we hypothesized that the benthic prey items will constitute a larger percentage of fish diet with size and that the ratio of benthic prey will increase with size more quickly in darker lakes.

## **Methods**

This study was conducted at the University of Notre Dame Environmental Research Center, Wisconsin, USA. The two study lakes were Crampton Lake, with low DOC (approximately 5 mg/L) and Hummingbird Lake, with high DOC (approximately 19 mg/L).

Yellow perch and bluegill were obtained from Crampton and Hummingbird lakes using minnow traps in June 2015. The data collected were supplemented with additional samples from the summer of 2012. Sixty yellow perch and 91 bluegills were caught in Crampton. Seven yellow perch and 28 bluegills were caught in Hummingbird. Fish length and weight were measured, and fish stomachs were flushed using gastric lavage. Stomach contents were preserved in 70% ethanol.

Stomach contents were identified, and the size of prey items was recorded. Prey items were classified to order or class and grouped as pelagic, benthic or terrestrial. Benthic items included hydrachnidae (water mites), hemiptera, oligochaetes, and aquatic insect larvae such as

chironomids, sialidae, trichoptera, odonata, and ephemeroptera naiads. Pelagic prey items included chaoborus larvae and pupae, cladocerans and chironomid pupae. Terrestrial prey consisted of terrestrial coleoptera, adult diptera, arachnids and one zygotera adult. The dry weight of identified prey items was calculated from the measured body length or head width (See Appendix). When no size information was measurable for dry mass conversions, the average size of the prey item category was used as a body length for mass calculations. Dry mass was used to compare proportions of prey types as dry mass has been shown to be a better estimate of abundance than individual counts (Hyslop 1980).

Total dry biomass for each fish stomach was calculated and standardized according to fish length. Relative mass of stomach contents was compared between all caught fish in Crampton and Hummingbird lakes using an independent two-sample t-test. To identify any differences in the source of stomach contents between bluegill and yellow perch, an independent two-sample t-test was run for each species comparing percent fullness of pelagic and benthic prey in each lake. I conducted regression analyses using all fish caught in each lake to identify relationships between fish length and the proportions of benthic and pelagic prey dry weight masses in diets. Finally, I ran the same regressions separating the two fish species.

## Results

The average size of fish caught in Crampton Lake was  $76.0 \pm 4.4$  mm (mean  $\pm$  SD), while in Hummingbird Lake the average length of fish caught was  $78.3 \pm 31.9$  mm (Table 1). Crampton fish showed less deviation from the mean (Figure 1).

A t-test revealed that fish in Hummingbird Lake have significantly higher stomach fullness relative to fish length than fish from Crampton ( $p < 0.041$ ). When the fish species were analyzed separately, bluegill in Hummingbird had higher relative stomach fullness than in

Crampton ( $p < 0.014$ ). Yellow perch showed slightly higher relative stomach fullness in Crampton Lake, but the difference was not significant ( $p = 0.057$ ; Fig. 2)

When diet composition was analyzed, Hummingbird fish showed a higher percentage of pelagic diet mass than Crampton fish ( $p < 0.001$ ). Separation of the two species showed a slightly higher fraction of benthic prey in Crampton bluegill, but the difference was not significant ( $p = 0.135$ ; Fig. 3). However, Hummingbird bluegill had a significantly higher percentage of pelagic stomach contents than Crampton bluegill ( $p < 0.001$ ; Fig. 4). Yellow perch showed no significant difference in benthic ( $p > 0.05$ ) and pelagic ( $p > 0.05$ ) stomach contents between the two lakes (Figs. 5 and 6).

A regression relating benthic diet proportion (benthic DM/ total DM) of each species of Crampton Lake fish to fish length showed no significant relationship ( $p > 0.05$ ; Fig. 7). The same test with pelagic diet proportion did, however, show a positive relationship between bluegill pelagic feeding and body length in Crampton Lake ( $R^2=0.051$ ,  $p<0.033$ ) and a negative relationship between yellow perch pelagic feeding and body length ( $R^2=0.108$ ,  $p<0.012$ ; Fig. 8). Both relationships, however, show low goodness-of-fit values suggesting weak relationships at best. In Hummingbird Lake fish, there was no significant relationship between benthic diet proportion and fish body length ( $R^2<0.10$ ,  $p>0.05$ ; Fig. 9) or between pelagic diet proportion and fish body length ( $R^2<0.10$ ,  $p>0.05$ ; Fig. 10) when each species was analyzed separately. Regression analyses showed no significant relationship between prey choice and fish size when fish were grouped together for either lake (all  $R^2<0.10$ , all  $p> 0.05$ ). Tables 2 and 3 include all statistical results.

## Discussion

This experiment sought to test the hypothesis that in Hummingbird Lake (high DOC), benthic items will compose a larger part of fish diet compared to Crampton Lake (low DOC) due to reduced visibility for pelagic hunting. Our study showed the opposite to be true: the stomachs of Hummingbird fish had a higher proportion of pelagic stomach contents than Crampton fish, a difference driven primarily by increased pelagic feeding by bluegill. We also hypothesized that the proportion of benthic prey items in the fish diets will increase with size more quickly in dark lake fish than in clear lake fish. A regression relating pelagic prey item proportion to fish body length showed a negative relationship in Crampton yellow perch but a positive relationship in Crampton bluegill. There was no other significant relationship between benthic or pelagic diet proportion and fish size in either lake or in either species.

The high proportion of pelagic food resources observed in Hummingbird fish, comprised largely of zooplankton, may be due to increased abundance of zooplankton in the epilimnion of humic lakes. It has been suggested that zooplankton populations benefit from increased DOC in lakes such as Hummingbird due to increased heterotrophic bacteria productivity (Salonen and Hammar 1986, Nürnberg and Shaw 1999). This effect is especially apparent in lakes with high allochthonous input like Hummingbird where bacterioplankton are required to release carbon from terrestrial sources (Jansson et al. 2000). Studies have shown that humic lakes with shallow stratification aid diel migration and provide easy access to food resources at or below the thermocline (Salonen and Lehtovaara 1992). Increased pelagic feeding by bluegill occurs despite this supposed zooplankton advantage in humic lakes. Our results suggest that high-DOC waters may provide preferable habitat for zooplankton, providing a pelagic food resource plentiful



enough to counteract visual limitations on fish hunting. Even if there is growing evidence that high input of terrestrial compounds limits productivity in lakes (Kelly et al. 2014), these studies show that changes to lake structure from high DOC concentration may have the effect of concentrating zooplankton into a viable food source. Zooplankton sampling at the two lakes may identify differing densities to support this analysis.

Lake size is one possible variable that could have contributed to increased feeding in Hummingbird Lake. Though the two study sites were chosen based on DOC concentration, Crampton Lake is much larger (25.8 ha) and deeper (15.2 m) than Hummingbird Lake (0.76 ha and 7 m; Craig, verbal communication). Studies on bluegill have shown that feeding switches in bluegill are largely dependent on the presence of large predators and that predation risk is the main limitation to pelagic-zone zooplankton feeding (Werner and Hall 1988). Juvenile bluegill in the Crampton, a large fishing lake, are likely exposed to far more piscivorous fish than in small, humic Hummingbird Lake and would be less likely to have a high proportion of pelagic prey stomach mass. Further study would require sampling several clear and dark lakes of different sizes to isolate DOC effects on feeding from effects of lake size.

Pelagic feeding decreased with fish length as predicted in Crampton bluegill, but the relationship has a low goodness-of-fit ( $R^2$ ) value, and there was no significant trend in Hummingbird to compare relationships between the two lakes. This is consistent with Allen's study (1935) showing a marked decline in pelagic stomach contents of bluegill with increasing body length. The same study found that bluegill only switch to primarily bottom-feeding organisms upon reaching 11.5 cm in length (Allen 1935), but only one bluegill caught in Crampton Lake was over 11.5 cm in length. This would account for the lack of a trend observed for benthic proportion and fish length. Lake size restricted the number of diets collected in

Hummingbird Lake; future study would sample a larger lake or several smaller lakes to better identify trends of fish diet and fish length related to DOC.

The positive relationship between pelagic feeding and fish length in Crampton yellow perch was unexpected, but a very low  $R^2$  value calls into question the strength of this relationship. When considering this relationship, it is important to note that, unlike in bluegill, the shift to adult feeding takes place in perch between five and nine cm long, and it is not only a transition to piscivory but also a return to pelagic zooplanktivory (Werner and Hall 1988). Of the sixty yellow perch caught in Crampton, twelve were nine cm or longer, and all but two were over five cm in length. The fish caught in Crampton were too large to see the initial shift to benthic foraging; the positive trend observed instead documents the second dietary shift back to pelagic feeding. Additional study in this area could plan data collection earlier in the year when juvenile fish would be smaller, or could investigate DOC effects on this second dietary shift. Again, effective comparison between humic and clear lakes will benefit from sampling larger lakes or several lakes of similar DOC concentrations. Results from diet composition comparison between lakes, however, suggest that future analyses of this dietary transition may show a different relationship than we originally predicted: namely, that pelagic feeding is favored in dark waters and that the transition to benthic foraging in humic lakes will not necessarily be earlier in fish development than in clear lakes.

Our study suggests that dissolved organic carbon does not necessarily negatively affect stomach fullness of freshwater fish. Though both yellow perch and bluegill rely on vision to hunt pelagic prey, it is clear that DOC affects many physical and biotic lake characteristics so that dark-water limitations on visual hunting matter less than other factors in determining fish diet. Findings that DOC reduces fish productivity (Karlsson et al. 2009) may have other causes rather

than visual hunting limitations. It is true, for example, that although zooplankton benefit from darker epilimnion, the depth of this layer is highly reduced in dark water and likely supports less biomass (Kelly et al. 2014). By integrating study of physical characteristics, primarily productivity, and multiple consumer levels, we can better understand DOC's effect on lake communities and plan for the effects of climate and land use changes on these ecosystems.

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		<b>Crampton</b>	<b>Hummingbird</b>
<b>Bluegill</b>	<b>Sample size</b>	91	28
	<b>Average fish length (mm)</b>	73.43 ± 13.96	74.52 ± 33.42
	<b>Total diet mass relative to fish length</b>	0.02 ± 0.04	0.07 ± 0.09
	<b>Proportion benthic</b>	0.69 ± 0.41	0.45 ± 0.37
	<b>Proportion pelagic</b>	0.11 ± 0.23	0.50 ± 0.38
	<b>Proportion terrestrial</b>	0.01 ± 0.10	0.02 ± 0.08
<b>Yellow Perch</b>	<b>Sample size</b>	60	8
	<b>Average fish length (mm)</b>	79.86 ± 14.29	93.21 ± 20.01
	<b>Total diet mass relative to fish length</b>	0.03 ± 0.07	0.01 ± 0.01
	<b>Proportion benthic</b>	0.45 ± 0.45	0.49 ± 0.45
	<b>Proportion pelagic</b>	0.27 ± 0.39	0.51 ± 0.45
	<b>Proportion terrestrial</b>	0	0

Table 1. Proportions of benthic, pelagic and terrestrial prey items in the stomachs of bluegill and yellow perch from Crampton Lake (low DOC) and Hummingbird Lake (High DOC). Proportions are averages ± standard deviation.



Species	Factor	t	df.	p
Bluegill	Stomach fullness	2.64	30	<b>*0.013</b>
	Proportion benthic	5.11	31	<b>*&lt;0.001</b>
	Proportion pelagic	1.53	40	0.135
Yellow perch	Stomach fullness	1.93	64	0.057
	Proportion benthic	0.10	8	0.924
	Proportion pelagic	0.92	8	0.386
All fish	Stomach fullness	2.11	41	<b>*0.041</b>
	Proportion benthic	0.86	48	0.396
	Proportion pelagic	4.55	43	<b>*&lt;0.001</b>

Table 2. Results of unpaired two sample t-tests, comparing factor (stomach fullness, length-adjusted benthic diet proportion or length-adjusted pelagic diet proportion) between Crampton and Hummingbird Lakes. A (\*) indicates a significant p-value.

	Species	Factor	Equation	R <sup>2</sup>	F	p
Crampton	Bluegill	Proportion benthic	$-0.0017x + 0.8156$	0.003	0.30	0.503
	Bluegill	Proportion pelagic	$0.0037x - 0.1656$	0.051	4.75	<b>*0.032</b>
	Yellow perch	Proportion benthic	$0.0015x + 0.3267$	0.0023	0.131	0.718
	Yellow perch	Proportion pelagic	$-0.009x + 0.99$	0.108	6.99	<b>*0.011</b>
	All fish	Proportion benthic	$-0.0022x + 0.7605$	0.005	0.77	0.383
	All fish	Proportion pelagic	$-0.0002x + 0.1867$	0.000	0.11	0.916
Hummingbird	Bluegill	Proportion benthic	$-0.0002x + 0.4702$	0.000	0.03	0.868
	Bluegill	Proportion pelagic	$-0.0015x + 0.5966$	0.010	0.33	0.571
	Yellow perch	Proportion benthic	$-0.0023x + 0.6631$	0.010	0.04	0.850
	Yellow perch	Proportion pelagic	$0.0023x + 0.3369$	0.019	0.04	0.850
	All fish	Proportion benthic	$-0.0003x + 0.4824$	0.001	0.03	0.870
	All fish	Proportion pelagic	$-0.0009x + 0.5705$	0.006	0.19	0.667

Table 3. Results of linear regressions of benthic or pelagic diet percentage with the independent variable fish length. A (\*) indicates a significant p-value.

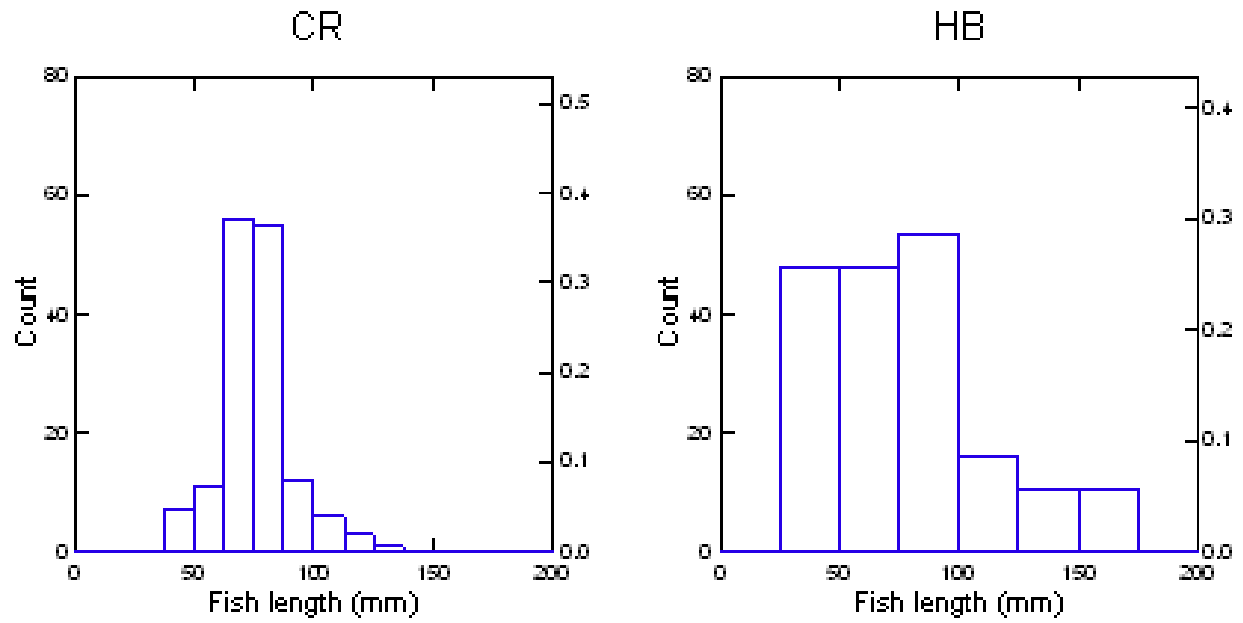


Figure 1. Frequency distribution histogram for fish caught in Crampton (CR) and Hummingbird (HB) lakes. Crampton fish lengths were more centered on mean (smaller SD).

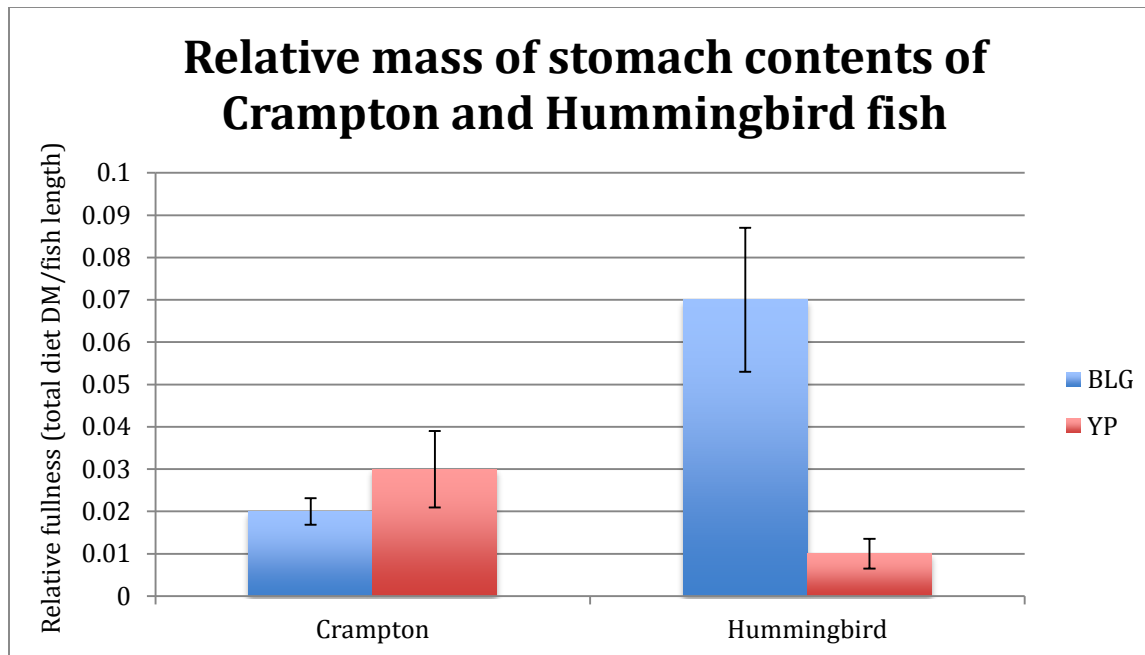


Figure 2. Fullness of fish stomachs relative to length of bluegill (blue bars) and yellow perch (red bars) in Crampton (CR) and Hummingbird (HB) lakes. Fish in Hummingbird were found to have relatively fuller stomachs ( $p < 0.05$ ), but when fish were evaluated separately only bluegill showed a significant disparity ( $p < 0.014$ ; yellow perch  $p = 0.057$ ). Error bars indicate standard error.

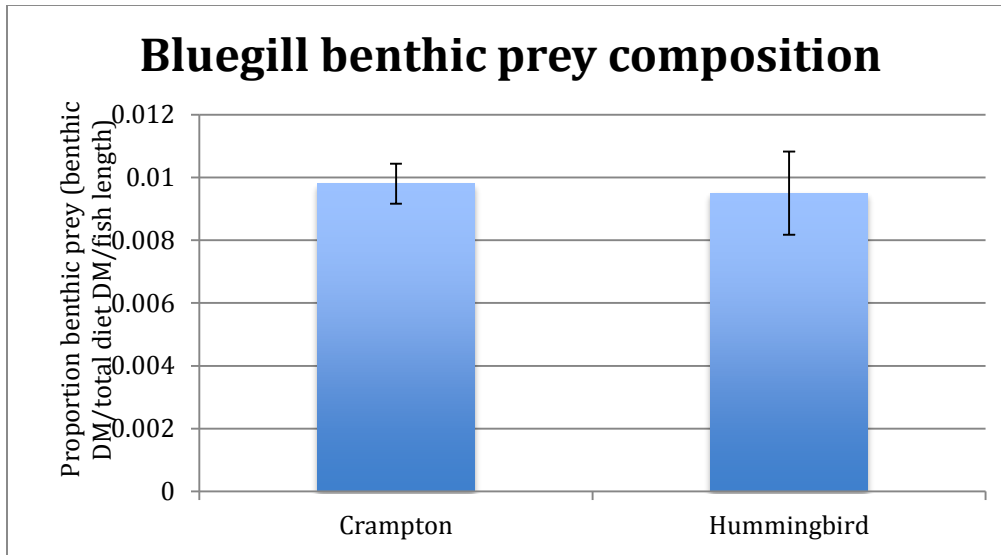


Figure 3. Fraction of bluegill stomachs filled with benthic prey (proportion of total mass adjusted for fish length) in each lake. No significant preference was shown for benthic prey in Crampton bluegill compared to bluegill in Hummingbird ( $p = 0.14$ ).

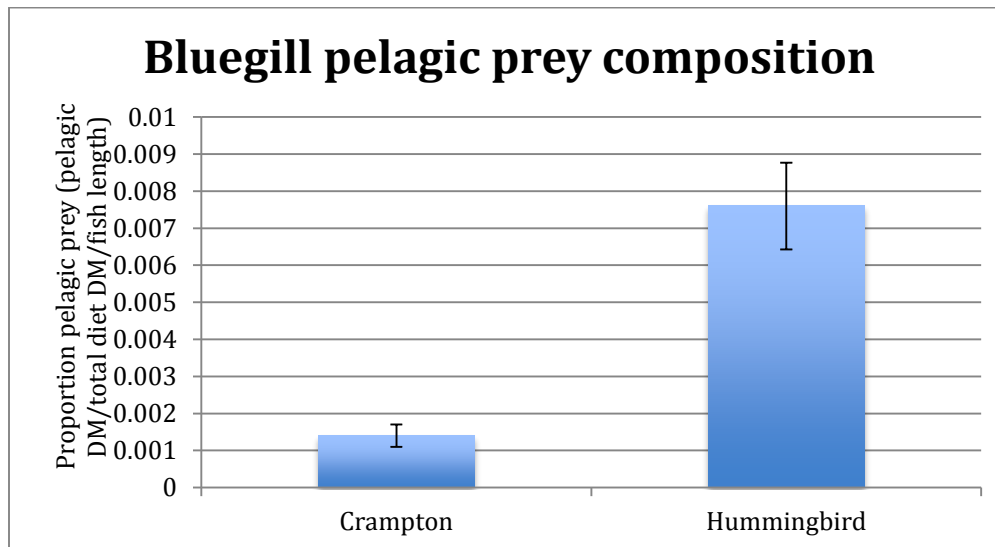


Figure 4. Fraction of bluegill stomachs filled with pelagic prey. Hummingbird bluegill had significantly more pelagic prey mass in their stomachs than Crampton bluegill ( $p < 0.001$ ). Error bars indicate standard error.

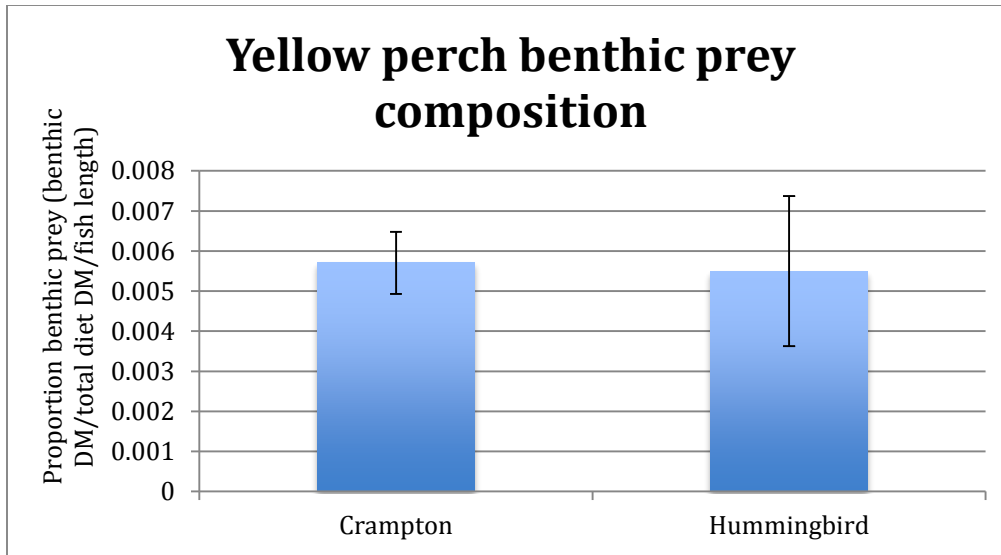


Figure 5. Fraction of yellow perch stomachs filled with benthic prey and (proportion of total mass adjusted for fish length) in each lake. No significant difference in benthic composition of fish diets between the lakes ( $p > 0.05$ ). Error bars indicate standard error.

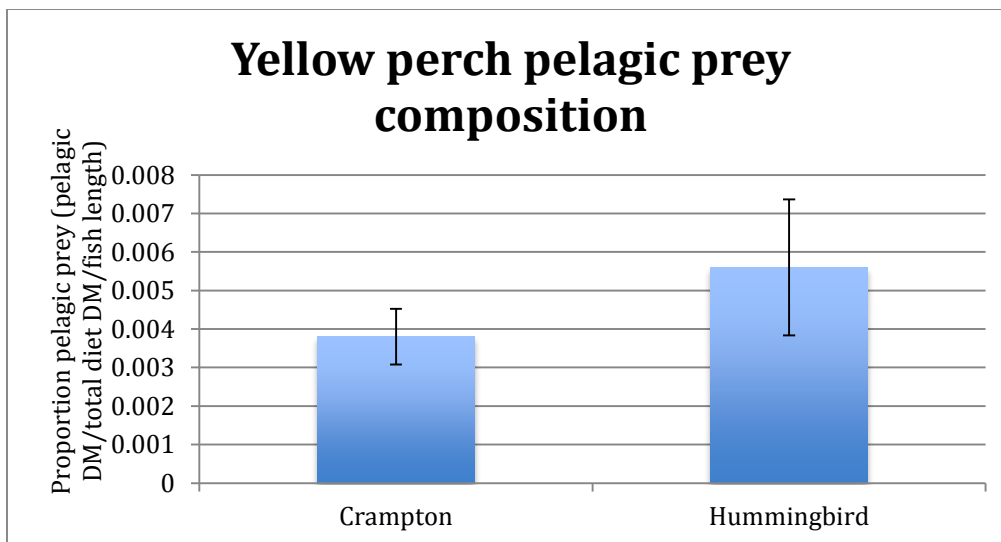


Figure 6. Fraction of yellow perch stomachs filled with pelagic prey and (proportion of total mass adjusted for fish length) in each lake. No significant difference in pelagic composition of fish diets between the lakes ( $p > 0.05$ ). Error bars indicate standard error.

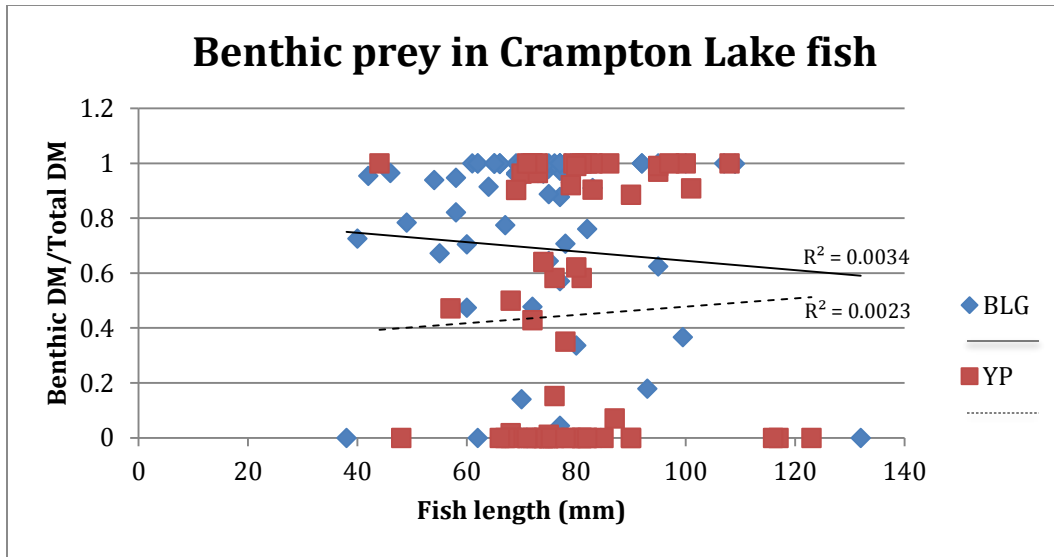


Figure 7. Proportion of benthic prey items in bluegill (BLG) and yellow perch (YP) in Crampton Lake. There was no significant correlation between percent benthic prey item by weight and fish length ( $p > 0.05$ ).

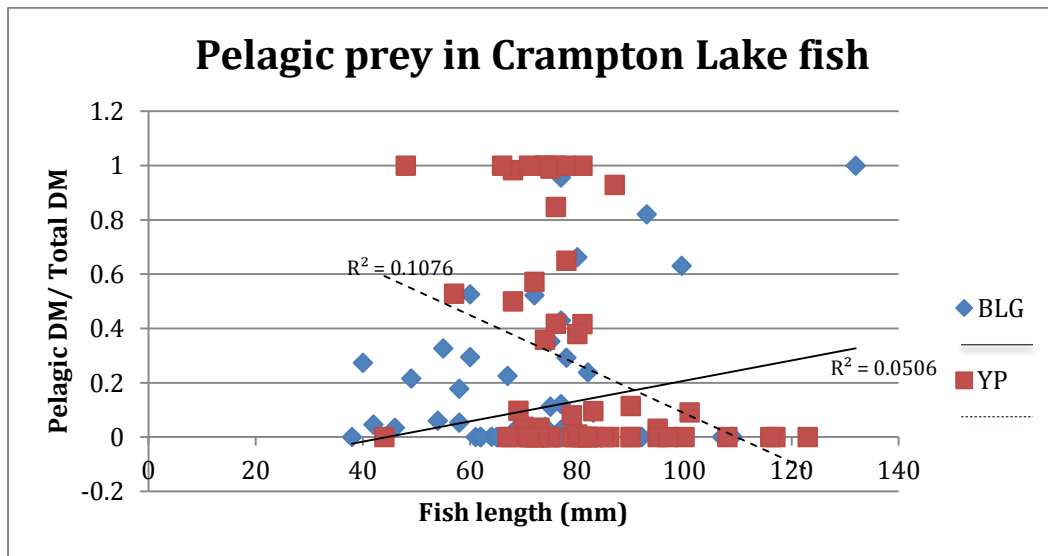


Figure 8. Proportion of pelagic prey items in bluegill (BLG) and yellow perch (YP) in Crampton Lake. Pelagic prey increased with size in bluegill ( $R^2 = 0.051$ ,  $p < 0.033$ ) and decreased with size in yellow perch ( $R^2 = 0.108$ ,  $p < 0.02$ ).

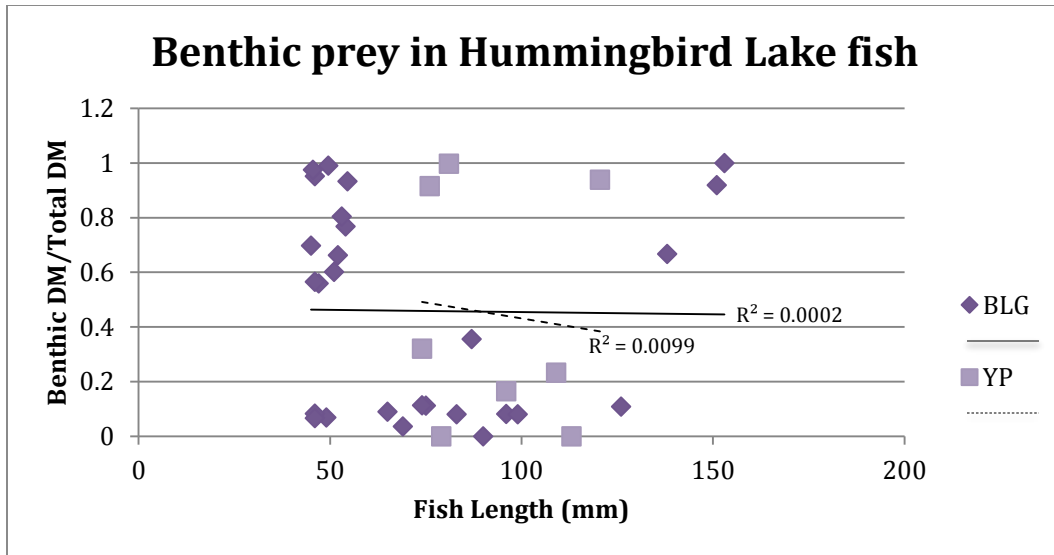


Figure 9. Proportion of benthic prey items in bluegill (BLG) and yellow perch (YP) in Hummingbird Lake. There was no significant correlation between percent benthic prey item by weight and fish ( $p > 0.05$ ).

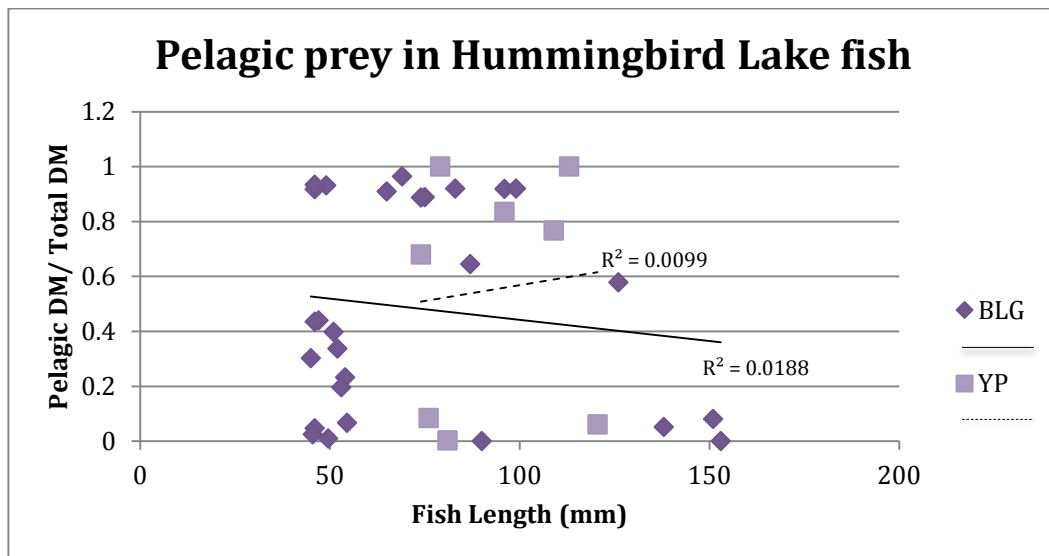


Figure 10. Proportion of pelagic prey items in bluegill (BLG) and yellow perch (YP) in Hummingbird Lake. There was no significant correlation between percent pelagic prey items by weight and fish length ( $p > 0.05$ ).

## Appendix: Equations

Prey Item	Equation	Reference
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_terrestrial	$DM=0.0077*L^{2.91}$	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)
Fish_unidentifiable	$DM=0.02118*L^{2.3473}$	Nikki Craig – unpublished data
Hydrachnidae	$DM=0.13265*L^{1.66}$	Baumgartner & Rothaupt (2003)
Hydroptilidae	$DM = 0.0056*L^{2.839}$	Marshall (2012)
Invertebrate_unidentifiable	$\ln(DM) = -7.761 + 0.34975*L + 0.0039315*L^2$	Sage (1982)
Oligochaeta	$DM=0.005888*L^{1.54}$	Methot et al (2012)
Sphaeriidae	$DM=0.0163*L^{2.477}$	Benke et al (1999)
Terrestrial_invertebrate	$\ln(DM) = -7.761 + 0.34975*L + 0.0039315*L^2$	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)
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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