Investigating a Proposed Habitat Squeeze on Largemouth Bass Due to Increasing Dissolved Organic Carbon Concentrations

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Abstract

Studies have shown that high levels of dissolved organic carbon (DOC) decrease fish productivity in small lakes, although the mechanism for the negative influence is not well understood. This study investigated the existence and influence of a proposed "habitat squeeze" mechanism by which decreased optimum fish habitat in high-DOC lakes causes increased fish population density. Increased population density can lead to problems like physical overcrowding and increased competition for scarce resources, and these effects resulting from habitat squeeze may contribute to the limitations on fish productivity imposed by high DOC levels. The thermal structure and largemouth bass behavior in two lakes with different DOC concentrations were compared to examine the influence of habitat squeeze on the lake with higher DOC levels. Thermal sensors and lake bathymetry data were used to demonstrate that the volume of water above the thermocline was smaller in the high-DOC lake than in the low-DOC lake. Temperature tags were attached to largemouth bass in the two lakes to study differences in bass depth-frequenting behavior. Data from reclaimed tags revealed that bass in the high-DOC lake generally spent time in shallower water than bass in the low-DOC lake. However, it was determined that bass in both lakes spent the vast majority of their time above their respective lake's thermocline. The bass behavior data and habitat calculations demonstrated that habitat squeeze increased the population density in the high-DOC lake by 16.83%.

Introduction

The effect of dissolved organic carbon (DOC) on lakes has become an important topic in environmental research over the last several decades. Global climate change has been linked to increasing DOC in lakes (Monteith et al. 2007). Therefore, it is important to study how DOC can affect lake ecosystems so that measures can be taken in the future to protect lakes and the resources they provide.

Most of the DOC in lakes results from the breakdown of plant matter (Karlsson 2003). As plants decay in the water, their carbon leaches into the lake, increasing the concentration of dissolved carbon per unit volume of water. DOC concentration is correlated to water transparency, with high-DOC lakes having a darker and distinctly brown color as compared to low-DOC lakes, which tend to be clearer (Jones 1992). The decreased transparency resulting from a high DOC concentration can have a profound effect on a lake's thermal profile (Read and Rose 2013). Northern temperate lakes tend be clearly stratified during the summer, meaning that there are three thermally distinct horizontal layers of water (strata) which make up the volume of the lake. In a stratified lake, the warm, bright, oxygen-rich epilimnion is separated from the cold, dark, oxygen-poor hypolimnion by the thermocline. Stratification occurs as a result of solar radiation. The sun's radiation provides light energy, which water absorbs as heat when solar rays contact a lake's surface. At deeper and deeper depths, less light energy remains unabsorbed (Wetzel 1983). Therefore, the deep waters constitute the cold hypolimnion, while the shallow waters constitute the warm epilimnion.

Research has shown that DOC negatively affects the depth of the thermocline in small lakes (Read and Rose 2013). In, other words, a higher DOC concentration can lead to a shallower thermocline. As noted earlier, dissolving organic carbon in water makes the water darker. Due to the nature of light and pigments, darker water is more effective at blocking light transmission. This attenuation of solar radiation by higher DOC concentrations restricts the radiation's warming effects to shallower water, resulting in a shallower thermocline. Therefore, dark, high-DOC lakes tend to have smaller volumes of water above their thermoclines than clear, low-DOC lakes.

Largemouth bass (*Micropterus salmoides*) are known to thrive in the warm temperatures found above the thermocline (Oster 1983). A predatory fish which typically weighs less than four kilograms, the largemouth bass is among the most common and widespread predatory fish in North America (Oster

1983). Its role as a keystone species and apex predator in many freshwater systems (Carpenter and Kitchell 1993), as well as its economic value as a favored game fish for many anglers, makes it an important species on which scientific focus should be placed.

The fish productivity of dark lakes has been found to be less than that of clear lakes (Karlsson 2009). However, the mechanism of this productivity deficiency is not entirely understood (Finstad 2014). Because research has demonstrated that DOC can shrink the warm, oxygen-rich, livable layer of water above the thermocline, it is possible that fish production in dark lakes is decreased due to a decreased volume of optimum habitat. Having a smaller habitat, and thereby an increased population density, can put pressures on a population of fish including physical overcrowding and increased competition for decreased resources. These pressures can negatively impact productivity (Houde 2008). Because its preferred habitat is the warm and oxygen-rich layer of water above the thermocline, the largemouth bass may be susceptible to habitat loss and its negative repercussions due to a raised thermocline in high-DOC lakes. The specific question of this research project will be to determine whether or not largemouth bass in a high-DOC lake are indeed subject to this proposed “habitat squeeze” mechanism by which a shallower thermocline increases their population density. The alternate possibility is that bass do not strictly adhere to their optimum habitat and a shallower thermocline does not cause an increase in population density. If the habitat-squeezing mechanism does occur, it is likely to be a factor which influences the decreased fish production observed in high-DOC lakes. Better understanding the behavior of fish communities in high-DOC lakes will help environmental managers to create regulations that better protect the important resource that fish provide, now and in the future when DOC concentrations in lakes are likely to continue to rise (Monteith et al. 2007).

Methods

All research was conducted on Long Lake, an 8.9 hectare lake located at the University of Notre Dame Environmental Research Center (UNDERC) in Gogebic County, Michigan. An impermeable curtain divides Long Lake into two similar basins, called East Long Lake and West Long Lake. Past experimentation shows that this division causes the DOC concentration in East Long to increase more rapidly than the DOC concentration in West Long (Christensen et al. 1996). Because the impermeable curtain has been in place since 2012, the concentration of DOC in East Long (12 mg/L) was nearly double the DOC concentration in West Long (6 mg/L) during June and July 2014 (unpublished Jones-Weidel-Solomon Lab data).

To determine if the bass in East Long experience habitat squeeze due to the effects of DOC on the basin's thermal profile, temperature data was collected from fish in both basins to assess and compare their habitat usage. Temperature data was collected in two ways. First, data about the fish's habitat usage was collected through a tag-and-reclaim program. iButton thermochron™ tags were attached to twenty largemouth bass in each basin (for a total of forty tagged bass) in May and June 2014. These tags were then reclaimed through angling during June and July 2014. Each tag recorded water temperatures at ten minute intervals for up to fourteen days after activation.

While fish data collection was underway, researchers in the Jones-Weidel-Solomon Lab used sensors to measure the water temperature in the basins as a function of depth. These measurements were used in conjunction with complimentary Long Lake bathymetric volume data to calculate the volume of water above the thermocline in each basin. The thermocline was defined as the depth at which temperature declined most rapidly (Wetzel 1983). This calculated volume of the volume above the thermocline in each basin served as a quantification of the available optimum largemouth bass habitat provided by each basin.

Once all fish and limnological data were collected, they were statistically and computationally analyzed. First, the sensor-constructed thermal profiles of each basin were used to convert each temperature recorded from each fish from the tag-and-reclaim program into a depth from the surface. This transformation allowed for fair comparison between fish reclaimed from the two basins by eliminating the difference in thermal structure between the basins. The recaptured fish were sorted into periods during which their data recording overlapped. All comparison was conducted within these overlap groups to avoid any differences in depth preferences due to seasonal temperature variation and fish behavior changes. T-tests were performed between every combination of fish in each overlap period to assess differences in depth preferences between individuals.

In addition to the t-tests, the tag-and-reclaim data was used to compute the optimum habitat density in each basin. "Optimum habitat density" (OHD) refers to the average density of a basin's largemouth bass population above the thermocline, as estimated by the depth data from the tagged *Micropterus* individuals. OHD was calculated by the equation

$$OHD = \frac{(Proportion\ of\ Recorded\ Depths\ Falling\ Above\ Thermocline)\cdot(Estimated\ Basin\ Population)}{Volume\ Above\ Thermocline}.$$

The estimated basin populations came from unpublished Jones-Weidel-Solomon Lab data. The distribution of the temperature data from the backup collection method was used to support the calculation of the proportion of tag-recorded depths falling above the thermocline in each basin. The OHDs in each basin were compared to shed light on the possible existence of habitat squeeze in East Long.

Results

Temperature sensor data collected by the Jones-Weidel-Solomon Lab was used to construct a thermal profile of each basin. A t-test of the depth of the thermocline in each basin, as recorded every ten minutes over a period from June 1 to July 9, demonstrated that the thermocline in East Long was, on average, significantly shallower than that of West Long ($p<.001$, $t=45.401$, $df=10882.101$) (Figure 1). The mean thermocline depths over this period in East and West Long were 1.93m and 2.22m, respectively.

Eight tagged fish were recaptured through the tag-and-reclaim program. Six of these fish were from East Long, while two were from West Long. Due to the tagging and recapture dates, there were two periods of overlap greater than one day between fish captured from the two basins. Fish 3, 4, and 6 from East Long overlapped with Fish 1 from West Long from 13:30 June 17, 2014 to 18:00 June 23, 2014. These same three fish from East Long overlapped with Fish 2 from West Long from 17:50 June 27, 2014 to 18:30 July 1, 2014. T-tests of the fish depths demonstrated that the fish in West Long generally spent time in water that was, on average, deeper than that inhabited by their East Long counterparts. This trend was significant in five of the six comparisons made between East and West Long fish (Table 1). Only Fish 6 from East Long did not spend time in significantly less deep water than the fish from West Long in its period of overlap.

There was also overlap between fish captured from the same basin. While no overlap occurred between the two fish reclaimed from West Long, there were substantial periods of overlap between the fish reclaimed from East Long. Fish 3, 4, and 6 overlapped from 13:30 June 17, 2014 to 18:30 July 1, 2014. Fish 1, 2, and 5 overlapped from 13:20 June 3, 2014 to 16:20 June 16, 2014, and Fish 2 and 5 overlapped slightly longer, with their range of coincidence extending from 13:20 June 3, 2014 to 18:40 June 17, 2014. T-tests of the fish depths demonstrated that each fish reclaimed from East Long displayed significantly different depth-frequenting behavior from the other East Long fish in its period of overlap (Table 1).

The fish depth data shows that the tagged bass almost never traveled to depths below their respective basin's thermocline (Figure 2). Of the 12,133 depths corresponding to temperatures recorded from fish in East Long, 99.984% were above the thermocline (Fish 1 and Fish 6 each crossed the thermocline once for less than twenty minutes apiece over the course of thirteen and fourteen days of tagging, respectively). Similarly, 100% of the 2,574 depths frequented in West Long were above the thermocline. Using these proportions, the OHD in East Long was calculated at 0.0130 fish/m^3, and the OHD in West Long was calculated at 0.0101 fish/m^3. While these results accurately portray the situation studied in Long Lake, the difference in whole-basin bass density between the two basins makes these numbers a poor indicator of the extent of the habitat squeeze present. At the time of the most recent estimates, East Long had a whole-basin bass density of 0.0052 fish/m^3, while West Long had a whole-basin bass density of 0.0047 fish/m^3. To account for this Long Lake bias, the OHD for East Long was multiplied by $\frac{0.0047}{0.0052}$, resulting in an adjusted OHD of 0.0118 fish/m^3. This adjusted OHD in East Long was 16.83% greater than the OHD in West Long and would be accurate in an ideal system in which East and West Long had equal whole-basin bass densities.

Discussion

The thermocline depth results support Read and Rose (2013), who demonstrated that increased DOC concentration decreases the depth of the thermocline in small lakes. The mean thermocline depth in East Long was 0.29m shallower than that in West Long over the course of the study, a substantial difference in depth when the volume of optimum habitat lost is considered. This means that if fish were relegated to their optimum thermal habitat in East Long to the same extent as in West Long, a habitat squeeze would have increased the population density of bass in East Long.

It was possible that the fish in East and West Long would exhibit similar depth-frequenting behavior, meaning that the fish in East Long would have been spending some time close to and below the basin's shallower thermocline. However, the t-tests between recaptured fish depths from East and West Long demonstrated that this was not the case. In five of six of these t-tests, the bass from East

Long spent time in significantly shallower water than the bass from West Long (Table 1). The fact that the fish in West Long were able to spend time in deeper water suggests that the fish in East Long were limited in their ability to live in similarly deep water by the inhibiting presence of a shallower thermocline.

The effect of the habitat squeeze occurring in East Long was quantified with the calculation of the two basins' OHDs. The adjusted OHD in East Long best represents the degree of influence exerted by the habitat-squeezing mechanism in that basin because it removes the initial confounding bias of East Long's higher whole-lake fish density. The 16.83% increase in bass population density in East Long's optimum habitat due to the shallower thermocline serves as a concrete indication that habitat squeeze increases population density in high-DOC lakes. The negative relationship between DOC concentration and thermocline depth in small lakes indicates that lakes with DOC concentrations higher than East Long's would experience an even greater loss of optimum habitat per unit area (Houser 2006). If bass continued to be limited to the shallow water above the thermocline in these lakes, the effect of habitat squeeze on their fish productivity would most likely be greater than the mechanism's effect in East Long. Further investigation into the specific relationship between fish population density and productivity would allow for more precise prediction of this mechanism's limiting influence on the fish productivity of other lakes on a DOC gradient.

Interestingly, despite the clear presence of habitat squeeze, biological productivity in East Long did not appear to be less than that in West Long over the course of the study. Surveys conducted by the Jones-Weidel-Solomon Lab indicated that largemouth bass in East Long consumed similar amounts of food, displayed equal ratios of weight to length, and grew at rates equal to their counterparts in West Long (unpublished lab data). Even productivity at other levels of the food chain in East Long was equal to or greater than that in West Long. Zooplankton, benthic invertebrates, and minnows in East Long showed no sign of decreased health or productivity due to the high DOC levels in the basin (unpublished lab data). Although East Long was not less productive than West Long, habitat squeeze may still have had a negative impact on its fish productivity. Studies have indicated that while very high levels of DOC are detrimental to a lake's productivity, moderate levels of DOC may actually provide certain benefits to fish populations in a lake (Finstad 2014). For example, small concentrations of DOC can provide energy subsidies, increase the amount of organic carbon in the food web, and shield fish from harmful UV-radiation (Hessen et al. 1990; Karlsson et al. 2012; Weidel et al. 2008; Williamson et al. 1996). It is entirely possible these factors have had a positive influence on fish productivity in East Long, cancelling out or overwhelming the probable negative effects of increased population density resulting from habitat squeeze. Finstad *et al.* (2014) demonstrated that fish productivity has a unimodal response to DOC concentrations, reaching a peak with moderate levels of DOC and then decreasing with higher concentrations. This study's findings of a concrete habitat-squeezing mechanism suggest that the increased effect of habitat squeeze in higher-DOC lakes may contribute to or directly cause the downwards slope in fish productivity observed by Finstad *et al.* (2014).

One interesting unintended result of this study was the observation of variance between individual behavior preferences in the tagged largemouth bass. T-tests between fish from the same basin during periods of overlap displayed significantly different depth-frequenting behavior. For example, Fish 4 from East Long lived .23m shallower on average than Fish 3 from East Long over the same period of overlap, a substantial difference in depth considering the depth of the thermocline was often between 1.5m and 2.5m. This study did not provide any evidence that would suggest why the fish exhibited significantly different behavior from one another. While the difference in behavior could be attributed to difference in tag attachment quality, all tagged fish were observed to be swimming regularly upon release and recapture, and no recaptured fish showed signs of excessively bad internal health or external infection. Further studies into the individual depth-frequenting behavior of largemouth bass and other species as a function of size, age, sex, or other factors may yield valuable scientific findings.

It is important to understand the limitations of this study. While large amounts of depth data were collected for each reclaimed fish, there was a small sample size of eight individuals, only two of which were from West Long. So although it can be said with certainty that the individuals studied demonstrated significantly different behavior, and that five of six comparisons between overlapping bass showed that the bass in East Long are relegated to shallower water than those in West Long, it is difficult to say with certainty that these trends hold true for the rest of the fish in Long Lake. The evidence of variance between behaviors of individuals in the study makes the findings less stable, because it is possible that the fish reclaimed in the tag-and-reclaim program may have behaved quite differently from the average fish in East and West Long. However, the large sample size of the depth data (14,707 total depth recordings) and the near-absoluteness of its tendency to be above the thermocline provide a strong indication that the population of bass spends the vast majority of its collective time above the thermocline. Confidence in the overwhelming tendency of the basins' bass populations to stay above the thermocline indicates confidence, too, in the 16.83% population density-increasing influence of the habitat squeeze occurring in East Long. Many factors in limnology could influence the presence and extent of habitat squeeze in other lakes. Nevertheless, this study provides the first high-frequency record of habitat use behavior in largemouth bass and compelling evidence that thermocline depth limits habitat availability in this species. Further studies, especially those on other northern temperate lakes along a DOC gradient, would help to clarify the influence on habitat squeeze on other species and other lakes.

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Table 1: Results of T-Tests between Reclaimed Bass during Periods of Overlap. The data from the fish followed by (a), (b), or (c) was cut down so that the t-test only used data from a concise period of overlap. If no letter in parentheses follows a fish's label, the data from the fish was not truncated for that t-test. The periods of overlap are as follows:

(a): 13:30 June 17, 2014 to 18:00 June 23, 2014

(b): 17:50 June 27, 2014 to 18:30 July 1, 2014

(c): 13:20 June 3, 2014 to 16:20 June 16, 2014

Fish 1	Fish 2	p-Value	t	df	Fish 1 mean	Fish 2 mean
East3(a)	West1	<0.001	-11.254	1743.964	0.583	0.846
East4(a)	West1	<0.001	-18.479	1712.476	0.424	0.846
East6(a)	West1	<0.001	-20.795	1682.298	0.379	0.846
East3(b)	West2(b)	<0.001	-4.084	1142.543	0.640	0.752
East4(b)	West2(b)	<0.001	-21.420	955.686	0.237	0.752
East6(b)	West2(b)	0.653	0.449	1136.769	0.765	0.752
East1	East2(c)	<0.001	4.759	3776.119	0.898	0.818
East1	East5(c)	0.006	2.740	2741.736	0.898	0.854
East2	East5	0.010	-2.580	4039.742	0.795	0.835
East3	East4	<0.001	18.633	3981.145	0.545	0.313
East3	East6	<0.001	4.196	4090.549	0.545	0.488
East4	East6	<0.001	-13.902	3956.417	0.313	0.488

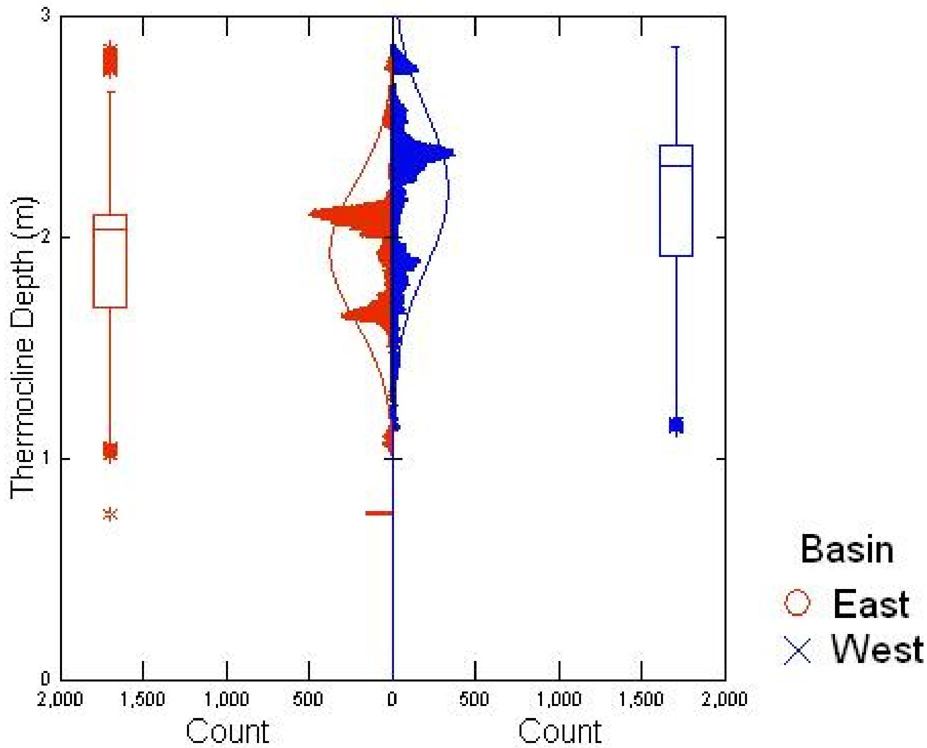

Figure 1: Thermocline Trends in East and West Long. The left side shows the distribution of recorded thermocline depths in East Long from 6/1/14 to 7/9/14. The right side shows the same for West Long. The peaks of the curved lines are located at each basin's average thermocline depth.

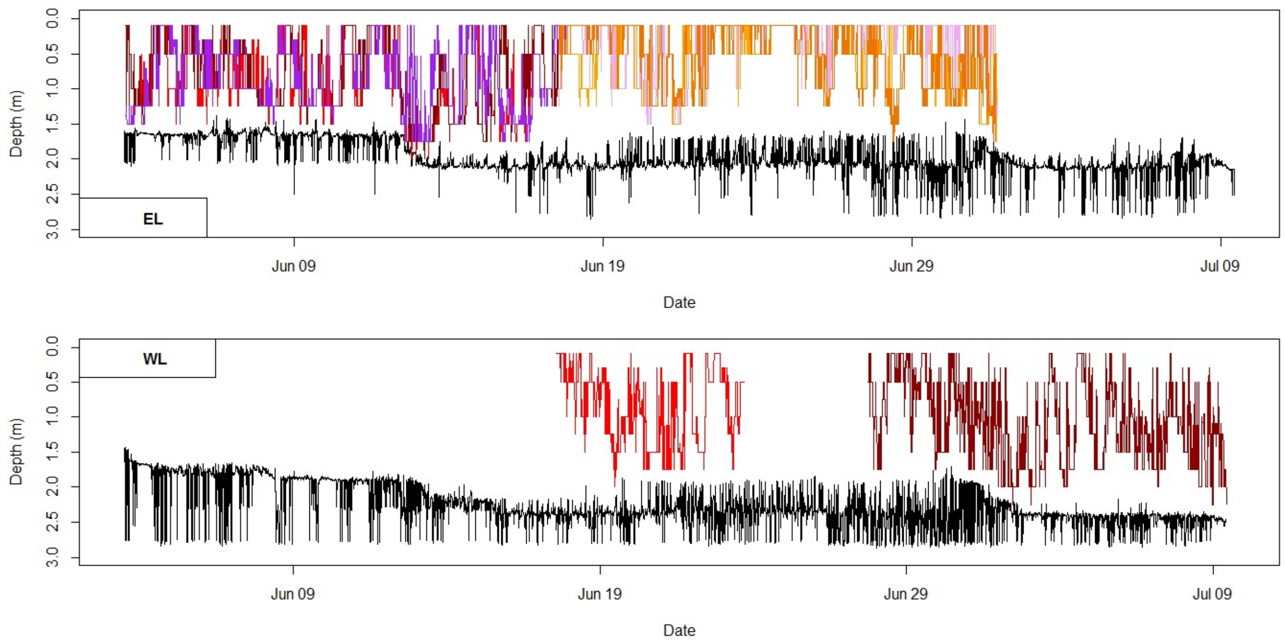

Figure 2: Fish Depths Frequented and Thermocline Depth over Time in East and West Long. The top graph displays the depths frequented by the fish reclaimed from East Long (the colored lines) and that basin's thermocline (the black line) from 6/1/14 to 7/9/14. The bottom graph displays the same for West Long. Each fish is represented by a differently-colored line.