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Filial cannibalism by largemouth bass (*Micropterus salmoides*): a three-decade natural history record from a small northern temperate lake

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ABSTRACT

We observed cannibalism by juvenile and adult largemouth bass (*Micropterus salmoides*) on their young-of-year (YOY) over nearly three decades (1984–2012) in a small temperate lake located in the Upper Peninsula of Michigan, USA. Largemouth bass are consistently the only fish species in the lake, necessitating the importance of studying filial cannibalism as a valuable energy source although it has potential consequences on recruitment and overall population structure. Annual whole-lake population estimates of juvenile and adult bass ranged 91–460 individuals, and these oscillations had significant differences between periods of higher and lower densities. Captured bass >150 mm in total length were individually tagged and had their stomach contents analyzed before being released. Despite significant differences in population estimates, we found no relationship with cannibalism. Additionally, we found no apparent patterns relating cannibalism to day of year, water temperature, or recruitment rates. We also found no differences in cannibalism or the size of consumed YOY between juvenile and adult bass. However, we found that recaptured individuals who consumed YOY bass on two or more occasions had significantly longer total length than individuals who consumed YOY bass one time or not at all, which provides additional evidence of dietary specialization as previously found in this population. Notwithstanding these patterns in cannibalism and the potential energetic benefits that it provides, we could not discern the effects of it on either individual growth rates or consequential changes in recruitment and overall population size. Regardless of the ever-present pressure of filial cannibalism, the population sustained recruitment across the whole study period.

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1. Introduction

The largemouth bass (*Micropterus salmoides*) is a keystone predator in lakes throughout eastern North America and southern Canada (MacCrimmon and Robbins 1975; Heidinger 1976). During the course of their lifespan, bass experience a series of ontogenetic niche shifts in both habitat and resource use (Olson 1996; Post 2003). Young-of-year (YOY) bass initially feed on zooplankton before transitioning to macroinvertebrate prey as they age (Gilliam 1982; Keast and Eadie 1985; Post 2003). In temperate lakes, many YOY bass transition to piscivory within the first year of life (Olson 1996). As a gape-limited predator, this shift to piscivory is size-dependent (Timmons et al. 1980; Hambright 1991) and the YOY must first reach a 2:1 size advantage over their prey (Lawrence 1958; Johnson and Post 1996). This shift to piscivory is typically accompanied by an increase in growth which may increase individual survivorship over winter and beyond (Summerfelt 1975; Timmons et al. 1980; Keast and Eadie 1985; Olson 1996; García-Berthou 2002). Juvenile and adult largemouth bass are also cannibalistic and opportunistically consume YOY prey (filial cannibalism) when they become seasonally available (Hodgson and Kitchell 1987; Hodgson and Hodgson 2000; Purdom et al. 2015). Individual YOY bass that hatch early in the spawning season, and/or experience rapid growth, can potentially obtain the size advantage necessary to practice intra-cohort cannibalism within their first year (Lawrence 1958; Olson 1996; Post 2003).

In northern lakes that support only populations of largemouth bass, the shift to piscivory within the first year is less likely to occur (Post 2003). Using stable isotope and direct diet analyses, Post (2003) found that relatively few YOY in these habitats were able to transition to and sustain piscivory during their first year of growth. However, when YOY are abundant, they represent an important dietary component for both adult and juvenile largemouth bass (Post et al. 1998; Hodgson and Hodgson 2000; Purdom et al. 2015). Additionally, there is a strong relationship between the number of reproductively mature adults and the number of nests and YOY that ultimately hatch (Post et al. 1998). In years in which the adult population density is high, there are typically more YOY and the intensity of inter-cohort cannibalism increases significantly (Post et al. 1998).

Cannibalism is common in numerous vertebrate species (Fox 1975; Bystrom et al. 1998; Payne et al. 2002; Rudolf 2007; Wissinger et al. 2010; Novosolov et al. 2013) and filial cannibalism is prevalent in teleost fishes (Manica 2002). Despite the direct decrease of conspecific population size from cannibalism, there are also potential benefits of this behavior from the individual to community level (Mock et al. 1990; Klug et al. 2006; Rudolf et al. 2010) and it may help stabilize both consumer and resource dynamics and contribute to the long-term stability of the population (Claessen et al. 2000, 2002). One effect of cannibalism on YOY bass is that it frees resources that would normally be consumed by that particular cohort. Cannibalism on the smallest size class would effectively increase the availability of zooplankton whereas, cannibalism on intermediate sized YOY would increase the availability of benthic prey (Persson et al. 2004). Cannibalism on their YOY may therefore increase the relative profitability of different resources and promote dietary specialization within the population (Andersson et al. 2007).

Dietary specializations are often documented through examination of *diet breadth* or the evenness of prey types ingested (Levins 1968). However, if the identity of the individual predator is known, the *diet consistency*, or tendency of individuals to select the same prey type over time can be determined (Schindler et al. 1997). Schindler et al. (1997) found that while diet breadth did not change with population size, the diet choice of individual largemouth bass was more consistent during years when the population density was high. Recent findings suggest that diet consistency in individual recaptured

largemouth bass (e.g. water mites and *Chaoborus* larvae) was the result of active selection of particular prey types rather than simple opportunistic encounters (Schindler et al. 1997; Hodgson et al. 2008; Rick et al. 2011). Individual foraging consistency may help bass exploit alternative resources during periods when intraspecific competition is intense and may explain how they are able to sustain relatively high population densities when their preferred prey (i.e. fish) is absent (Schindler et al. 1997).

In this study, we report on a 29-year natural history record (27 continuous years of marked and recaptured fish) of the population dynamics and occurrence of cannibalism for largemouth bass in Paul Lake, which is located in the Upper Peninsula of Michigan. The lake resides at the northern edge of the species' range and the foraging ecology of this population has been extensively documented (Hodgson and Kitchell 1987; Hodgson et al. 1993; Xe et al. 1994; Hodgson and Kinsella 1995; Schindler et al. 1997; Hodgson and Hodgson 2000; Post 2003; Hodgson and Hansen 2005; Hodgson et al. 2008; Rick et al. 2011; Purdom et al. 2015; Brosseau and Hodgson 2016).

However, none of these studies directly focused on the long-term pattern of cannibalism or examined whether certain members of the population exhibited cannibalistic dietary specializations for as long or as thoroughly as our historical survey. To date, the most detailed analysis of cannibalism in Paul Lake was limited to the 1993–1995 cohorts of YOY bass (Post et al. 1997, 1998; Post 2003). To our knowledge, such large (>5000 individual diets) and continuous (three decades) long-term data sets are relatively rare and we know of no other continuous foraging records that focus on cannibalism among largemouth bass of this duration. The population is relatively stable (reproducing adults found annually since 1976; Leavitt et al. 1989) and the lake consistently supports high population densities of small (<200 mm total length) to medium-sized (200 to >300 mm) bass. We provide estimates of the adult and juvenile population densities to determine if they were related with the intensity of cannibalism on the YOY during a given year. Because of the extensive record of individual diets, we were able to examine if a particular subset of the population specialized on YOY prey and determine if these individuals differed morphologically (size and mass) from others in the population. We also document the growth rate of a much larger sample of YOY bass collected over multiple seasons than has been previously reported for Paul Lake (Post et al. 1997, 1998; Post 2003).

Our data set provided a unique opportunity, *a posteriori*, to compare the growth rate of adult and juvenile bass collected during seasons in which cannibalism differed dramatically. Apart from the obvious benefit to the individual, cannibalism may also indirectly benefit other members of the population by increasing the profitability of different resources previously exploited by the YOY bass (Persson et al. 2004). We therefore expected to find higher seasonal growth rates during years in which the population density was low but cannibalism was high compared to those collected during years in which the population density was high and cannibalism was low.

2. Methods

2.1. Study site

Paul Lake is a small kettle (1.7 ha, max depth 15.0 m) and oligotrophic lake located in the Upper Peninsula of Michigan, USA (89°32'W; 46°13'N) on the property of University of Notre Dame Environmental Research Center (UNDERC). The property is a gated 3035 ha preserve not open to the public and the lake has been unmanipulated and unexploited since the early 1970s (Leavitt et al. 1989; Carpenter and Kitchell 1993). Large woody

debris in areas located near the shore provide cover for YOY bass. Apart from the rare episodic appearance of small numbers of pumpkinseed sunfish (*Lepomis gibbosus*) and various minnow species, Paul Lake supports a single-species fish community dominated by largemouth bass (>95% of the fish biomass at any one point). Paul Lake is connected via a culvert under an earthen dam to the adjacent Peter Lake, which has been manipulated over the years to host other fish species (Carpenter and Kitchell 1993). Despite the presence of netting on both sides of the culvert with mesh smaller than minnows, a very limited number of small fish have entered Paul Lake over the years. However, they never established reproductive populations, their presence was short-lived (J. R. Hodgson, personal observation), and they rarely appeared in gastric lavage samples (Purdom et al. 2015). For a more complete history of the lake see Leavitt et al. (1989) and Carpenter and Kitchell (1993).

2.2. Sampling protocol and diet analysis

Paul Lake has been studied extensively over three decades, and the largemouth bass population has been the reference point for numerous whole-lake trophic interaction studies (Carpenter et al. 1985, 1987, 1995, 2001; Carpenter and Kitchell 1993; Schindler et al. 1993). Central to the suite of those studies was the consistent and standardized largemouth bass capture, mark, and recapture sampling protocol across all years, which was further validated by Hodgson et al. (1989) and later reassessed by Cline et al. (2012). Largemouth bass (>150 mm TL, measured to the nearest 1.0 mm and weighed to the nearest 1.0 g) were sampled approximately every third week from May to August annually from 1984 to 2010. For each sampling effort, the water temperature of the lake was measured across 17 depths (0–10 m) where largemouth bass were typically found and the average water temperature was calculated. The mean annual sample size was 171 fish per year with a mean sample size of 22.7 fish per sampling effort. An average of seven samples were collected annually. Fish were collected from the littoral zone using angling and electrofishing methods. Angling methods employed light to medium spinning rods with bait hook sizes ranging sizes 2–5. All bass were either Floy or PIT tagged. Individual stomach contents were collected using gastric lavage similar to Seaburg (1957) and preserved in 95% ethanol within 1 h of capture. Specific diet sampling techniques are explained in greater detail in Hodgson and Kitchell (1987) and Hodgson et al. (1993). All fish were released after processing. Collectively, 5098 individual adult and juvenile largemouth bass stomach contents were sampled and 406,948 prey items were identified. Hodgson et al. (1989) found that increasing the sampling frequency within this protocol did not decrease intersample variance. For a more complete description regarding how these diet categories were combined into a series of functional groups for analyses see Purdom et al. (2015). For this study, we focused solely on cannibalism of YOY bass.

Since Paul Lake has been studied in this fashion for over three decades, it provides opportunities to ask questions *a posteriori* beyond the original whole-lake ecosystem monitoring, as is the case in the present study. However, this *a posteriori* approach also has limitations. For example, of the various studies spanning 1984–2010, none consistently measured the TL (mm) of YOY bass removed by gastric lavage. While not covering the entire study period, we took advantage of a separate protocol that did measure the length of YOYs in the stomach contents from 94 adult and juvenile cannibals collected between 2008 and 2012 in Paul Lake via gastric lavage (C. Buelo, unpublished data). We chose to include those data to augment our long-term analyses of 1984–2010 because these were our only source of consumed YOY TL (mm). We compared the TL (mm) of ingested

YOY consumed between the adult and juvenile size classes (detailed below) using the non-parametric Aspin-Welch *t* test. We also calculated the average TL (mm) of YOY consumed by month (June–August) using the non-parametric Kruskal–Wallis one-way ANOVA to determine how the size of the ingested prey differed across the season.

Additionally, we lack behavioral data (beyond dietary contents) and analyses of habitat heterogeneity. Therefore, another limitation of our *a posteriori* approach was our inability to address the questions of complex predator–prey interactions, especially prey vulnerability, within shared habitats and resources as asked and reviewed by Matter and Mannan (2005).

2.3. Population estimates

Annual whole-lake population densities of adult and juvenile bass (only fish >150 mm TL; calculated as the mean of mid-May and mid-August surveys) were estimated between 1984 and 2010 using the Schnabel method (Ricker 1975) on fish captured with boat-mounted electroshocking. Since Paul Lake is small (1.7 ha), we were able to sample a large proportion of the surface area, including the entirety of the littoral zone. This method was standardized and consistent over the duration of the study. We used SiZer (Significant Zero crossings; Sonderegger et al. 2009; Hodgson et al. 2013), which is a non-parametric method, to perform a time-series analysis of the yearly population density. SiZer employs a series of smoothing functions based on bandwidths around the data to statistically analyze the true modality and significant bifurcation points of the series. It does this by applying derivatives and analyzing significant zero crossings that indicate bifurcation points. This helped us identify periodic oscillations in population density that occurred throughout the study. We chose SiZer over other analyses because it does not violate any assumptions of parametric distribution or autocorrelations in time series (Rondonotti et al. 2007). We used the non-parametric Spearman's rank-order correlation to determine if annual fluctuations in population density were correlated with cannibalism, the percent change in annual cannibalism, the percent change in annual population density, the May–August average water temperature, and the recruitment rate of age-1 fish that survived their first winter (described below).

2.4. Size classifications

To distinguish between juvenile and adult size classes, we relied on Clady (1974) who also sampled largemouth bass from lakes in the Upper Peninsula of Michigan. Ideally, we would have been able to sacrifice individuals after gastric lavage to inspect their gonads to determine maturity, but we were constrained by the importance of marking and recapturing largemouth bass for the whole-ecosystem research on Paul Lake. As a workaround, based on Clady's findings, we classified individuals ≤ 229 mm TL as *juveniles* and those fish ≥ 230 mm TL as *adults*. We compared the total number of YOY consumed between 1984 and 2010 by both size classes using the non-parametric Aspin-Welch *t* test.

In addition to tagged fish that exceeded 150 mm, a total of 3805 smaller fish were collected during the study. Most of these fish were not subject to gastric lavage, but their total length (mm) was recorded prior to release. Some of these smaller bass that died during collection were subjected to gastric lavage or stomach dissection. Of the total 3805 smaller fish, 1820 were identified as YOY based on the findings of Post et al. (1998). They found that YOY in Paul Lake reached an average TL of 75 ± 10.7 mm by the end of August of their first year. We therefore classified any fish ≤ 86 mm in length as part of

that years' YOY cohort. Some of these fish collected between 1993 and 1995 were fin-clipped as part of a separate mark-recapture study reported previously (Johnson and Post 1996; Post et al. 1997, 1998; Post 2003). During the study, YOY were primarily collected during 1985–1989, 1991, 1993–1995, 2000, 2004, and 2006–2008. We sorted the TL (mm) of YOY collected by month across all years to determine their seasonal growth rate.

The remaining fish (1985) that were collected but not tagged ranged in length from 87 to 149 mm. We included these fish when calculating the average body length for all juveniles (87–229 mm) per season. We were also interested in estimating the annual recruitment of age-1 fish that had survived their first winter. To calculate recruitment, we used a conservative estimate that any fish with a TL = 88–125 mm was a 1-year-old fish that survived the winter (Post et al. 1998); 810 fish of these lengths were collected between 1984 and 2010. We divided the annual number of Age-1 fish collected by the total number of all fish sampled (87 mm-adult) for that particular year to calculate yearly recruitment.

2.5. General comparisons

To determine if cannibalism increased during the spawning season, we divided the sampling period into two 60-day periods (Julian Dates 135–195 and 196–256). The first half of the season (Julian Dates 135–195) coincided with the typical spawning activity of largemouth bass in Paul Lake (Post et al. 1998). The second half of the season (Julian Dates 196–256) contains little to no spawning activity; largemouth bass in northern temperate lakes typically spawn between late April and early July (Becker 1983). We compared the total number of YOY consumed and the total number of cannibals between these intervals using separate Aspin-Welch *t* tests.

A total of 13,329 adult and juvenile fish were tagged, processed and released across the study. Of these, 467 were subsequently recaptured with YOY in their stomach contents. We broke this group of recaptures into three categories: those that consumed YOYs on only one occasion; those that consumed YOYs on at least two occasions; and those that consumed YOYs on three or more occasions. For this analysis only, we conservatively discarded any data from cannibals who were only captured on one occasion (i.e. never recaptured). We compared the size (TL) of individuals from each of these groups with 1088 recaptured non-cannibals using the non-parametric Kruskal–Wallis one-way ANOVA and the Dunn's post-hoc test.

We were also interested in determining whether there was a difference in the growth rate of bass collected during years in which the frequency of cannibalism and the population density differed. We therefore examined data collected across three separate years that had the combination in which the population density was the lowest and the frequency of cannibalism was the highest. This data set was compiled from recaptured bass collected during 1992, 1994, and 1998 ($n = 273$). In each of these years, the estimated population density was below average (<253) yet more YOY were consumed than the average number (>146) for the entire study. We calculated the instantaneous growth rate (G_o) for recaptured adult and juvenile bass as described by Allen (1985):

$$G_o = \frac{100 \ln(W_2/W_1)}{t}$$

where W_1 and W_2 represent the weight of a particular fish during its first and second (last) collection of the season and t is the time duration in days between samples. We repeated this process for recaptured fish collected during 1997, 1999, and 2000 ($n = 309$). These were years that the population density was the highest and the frequency of

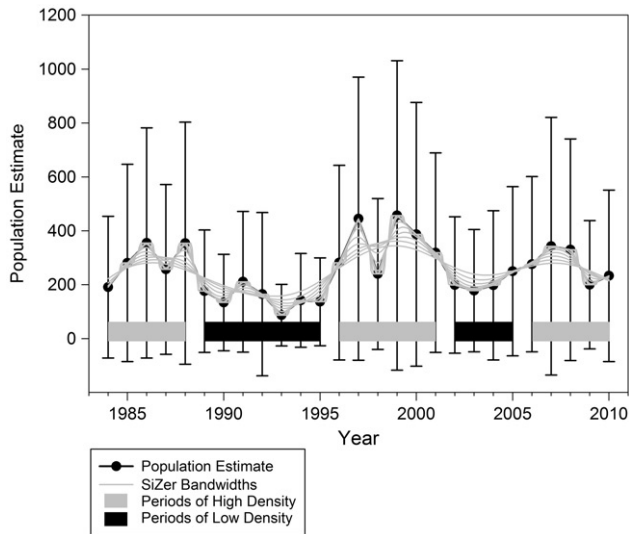


Figure 1. Annual adult and juvenile population density estimates with error bars (95% CI) and SiZer bandwidths used to determine significant differences between periods of high population and low population densities.

cannibalism was the lowest. We also calculated the percent change in length per day for each fish collected during either three-year interval. We compared the instantaneous growth rate and percent change in length for bass collected during these three-year intervals using separate Kruskal–Wallis one-way ANOVAs followed by the Dunn’s post-hoc test.

Due to our multiple analyses on this dataset, we Bonferroni corrected the critical alpha level for our entire study to 0.004 to minimize the probability of committing type-I errors. We were conservative in our approach by setting the initial critical alpha at 0.05 and correcting for 11 total analyses. Incidentally, none of our statistical results fell between probability levels 0.004–0.05; i.e. all cases of rejecting the null were <0.004 and all instances of failing to reject the null were >0.05 .

3. Results

The average whole lake population density of adult and juvenile largemouth bass was 253 (95% CI 218–334) with an annual density ranging from 91 (95% CI 71–114) in 1993 to 460 (95% CI 380–574) in 1999 (Figure 1). The results of the SiZer time-series analysis indicate a series of five intervals between 1984 and 2010 during which the population oscillated between periods of high and low density. Periods of high density occurred between 1984–1988, 1996–2001, and 2006–2010 (mean = 309, SE = ± 21.1). Periods of low density occurred between 1989–1995 and 2002–2005 (mean = 183, SE = ± 17.4). The average interval duration between each oscillation lasted 5.4 years. Overall, the population density from 1 year to the next was relatively stable falling within one standard deviation of the previous year’s Schnabel estimate for 19 out of the 27 years for which data were collected. Years in which the population density either increased or decreased by at least one-third of the previous year’s estimate include 1991, 1993, 1994, 1996, 1998, 1999, 2002, and 2009 (Table 1). During years in which the population density comparatively increased the most (1991, 1994, 1996, and 1999; +36%–51%), juvenile fish (≤ 229 mm) were collected in much greater numbers than adults (≥ 230 mm) (Table 1). In years in which the

Table 1. Shifts in the proportion of adult and juvenile fish following years in which the population density either increased or decreased by at least one-third of the previous year's estimate.

	1991	1994	1996	1999	1993	1998	2002	2009
% Change	+36	+39	+51	+47	-47	-46	-38	-39
% Juveniles	77	67	82	56	55	35	25	26
% Adults	23	33	18	44	45	65	75	74

population density dramatically declined (1993, 1998, 2002, and 2009; -38%–47%) the opposite was true and relatively few juveniles were collected (Table 1). We found no correlation between population density, total cannibalism, the percent change in annual cannibalism, the percent change in annual population density, the May–August average water temperature and the recruitment rate of age-1 fish that survived their first winter. The average annual recruitment of age-1 fish (87–125 mm) that survived their first winter was 7% (SE = ±1.8). There were 16 years in which recruitment was less than 5% and only four years in which it exceeded 10%. The strongest recruitment of age-1 fish occurred during 1995 (37%), 1993 (34%), and 1991 (21%).

A total of 13,329 fish were sampled as part of this study from the combined datasets spanning 1984–2010 and 2008–2012, and the stomach contents of 5098 of these were flushed and examined. The average largemouth bass collected was 214 g and 246 mm (TL) and the average cannibal was 229 mm (SE ±1.63) in length and consumed an average of 4.19 YOY per gut sample (range 1–105; SE ±0.27). Juvenile ($N = 420$) and adult ($N = 400$) cannibals consumed 1757 and 1675 YOY, respectively, in the 1984–2010 dataset. Combined with those numbers, 32 juveniles and 62 adult cannibals consumed 242 and 182 YOY, respectively, in the 2008–2012 dataset. In total for this study, 452 juvenile cannibals consumed 1999 YOY and 462 adult cannibals consumed 1857 YOY; 914 total cannibals consumed 3856 total YOY (Figure 2).

Cannibal size (TL) was highly variable, and while the majority of cannibals consumed <5 YOY each, there was no trend between the number of YOY in each individual gut sample and cannibal TL (Figure 2). Also, we found no difference between the total number of YOY consumed by the adult and juvenile size classes ($t = 0.008$, $p = 0.994$; Figure 2). Additionally, no differences in YOY consumption during the first half of the season (Julian Dates 135–195), corresponding with peak spawning activity, and YOY consumed during the second half of the season were found (Julian Dates 196–256) ($t = 1.91$, $p = 0.059$; Figure 3). While it would be expected that cannibalism should be greatest during spawning and maximum YOY availability, large differences in unequal variances caused us to reject any statistical significance. Furthermore, the total number of cannibals did not statistically differ between the first and second half of the season ($t = 0.705$, $p = 0.483$; Figure 4).

Using the smaller 2008–2012 dataset of 94 adult and juvenile bass that provided consumed YOY TL (C. Buelo, unpublished data), we found that adult cannibals appeared to consume larger YOY bass than juvenile cannibals. The average TL (mm) of 424 ingested YOY collected from the stomach contents these 62 adult and 32 juvenile cannibals between 2008 and 2012 is 14.91 mm (SE ±1.38) and 10.13 mm (SE ±1.69), respectively, but no significant differences were detected ($t = -1.72$, $p = 0.088$; Figure 5). Additionally, the largest YOYs appeared to be consumed in July (17.38 mm, SE ±3.19) compared to June (9.52 mm, SE ±1.36) and August (14.79 mm, SE ±2.19; Figure 6). Significant differences in consumed YOY TL by month were detected ($H = 18.9$, $p < 0.000$), but differences were not recovered in the post-hoc analysis (potentially due to small sample size and

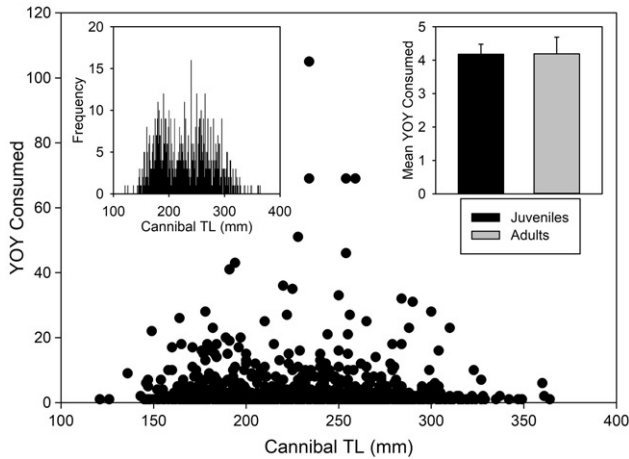


Figure 2. Cannibalism of YOY bass by adults and juveniles by body size (mm). Each data point represents the number of YOY in a single gut sample. The top left inlay graph is the length frequency of cannibals. No significant differences were found in cannibalism between juveniles and adults (top right inlay graph; $t = 0.008$, $p = 0.994$).

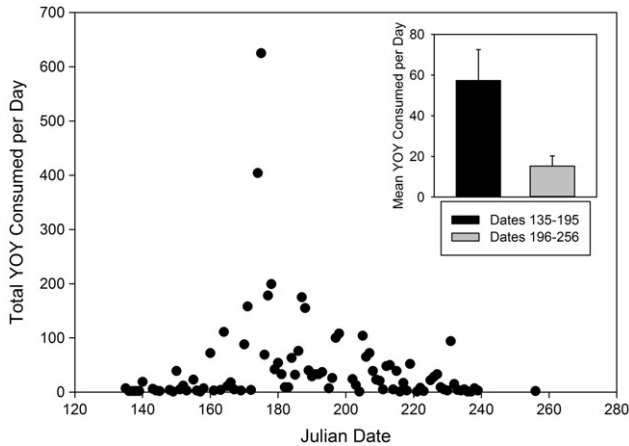


Figure 3. Total YOY consumed per Julian Date. No statistically significant differences in YOY consumption between the first half of the season and the second half were detected (inlay graph; $t = 1.91$, $p = 0.059$). Despite a difference in means, a 12-fold difference in variance resulted in failure to reject the null.

unequal variances) making this analysis unclear. However, intuitively, the seasonal growth for 1820 YOY between 1984 and 2010 increased throughout the summer months with a large increase after July (Julian date 212; Figure 7). The earliest date that YOY were collected was June 27 (Julian date 178). Only 15% of YOY reached lengths ≥ 60 mm ($n = 274$), and only 3% of these exceeded 70 mm ($n = 63$) by the end of their first year of growth.

A total of 467 adult and juvenile bass between 1984 and 2010 either had YOY in their stomach contents upon first collection or were later recaptured after having ingested YOY. Of those, 311 (67%) were found to have consumed YOY on only one sampling date. An additional 122 (26%) were identified as having ingested YOY on two sampling dates, while only 34 individuals (7%) had ingested YOY on at least three or more occasions. We compared the TL (mm) of individuals from these three categories with 1088 recaptured non-cannibals and found statistical differences between the groups ($H = 53.5$,

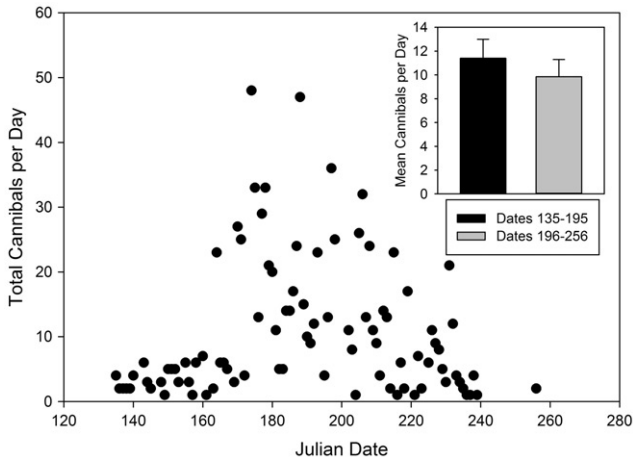


Figure 4. Total juvenile and adult cannibals per Julian Date. No significant differences were found in the number of cannibals between the first and second halves of the season (inlay graph; $t = 0.705$, $p = 0.483$).

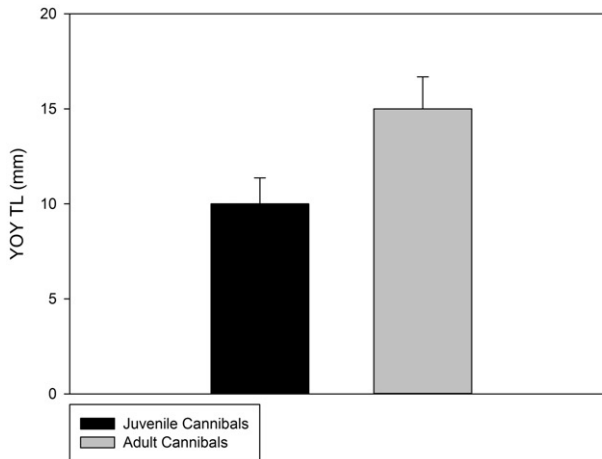


Figure 5. Average size of 424 consumed YOY by 94 juvenile and adult cannibals for fish analyzed from the subset of data between 2008 and 2012. No significant differences were detected ($t = -1.72$, $p = 0.088$).

$p = 0.000$). The results of the Dunn's post-hoc test indicate that individuals who ingested YOY on at least two or more occasions ($n = 156$) had significantly greater TL than individuals from both other groups (Figure 8). However, we found no difference in either the instantaneous growth rate (G_o) ($H = 0.93$, $p = 0.334$) or the percent increase in length/day ($H = 2.13$, $p = 0.884$) for individuals collected during years in which the population density was low and the frequency of cannibalism was high compared to years in which those conditions were reversed.

4. Discussion

Analyzing the long-term natural history observations of foraging by the monospecific largemouth bass assemblage in Paul Lake provided an unprecedented opportunity to investigate if cannibalism on YOY had any effects on overall population structure and dynamics. Paul Lake has had a continuous largemouth bass population since at least 1976

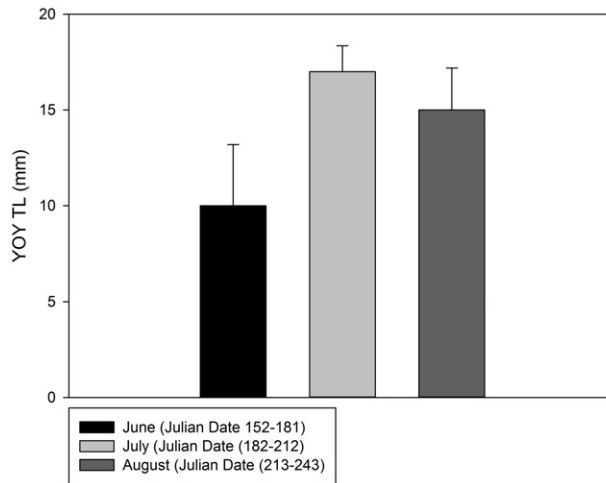


Figure 6. Average size of 424 consumed YOY by month fish analyzed from the subset of data between 2008 and 2012. Significant differences were found ($H = 18.9$, $p < 0.000$), but they could not be recovered in the posthoc analysis, making this analysis unclear.

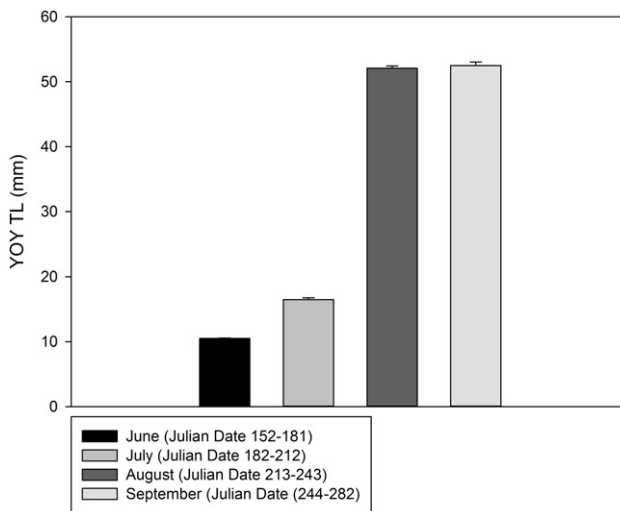


Figure 7. Seasonal growth (TL) for 1820 non-consumed YOY collected between 1984 and 2010.

(Leavitt et al. 1989), but the total lake population density of adult and juvenile bass in Paul Lake varied over three decades. Specifically, four significant bifurcation points separated periods of high and low densities, and each period lasted on average approximately 5 years. We expected that cannibalism would be a contributing factor to these changes in population size, as well as recruitment, body size and growth rate. However, we found no correlations among annual population density, total rate of cannibalism, percent change in either the annual rate of cannibalism -or- annual population density, May–August average water temperature, or recruitment rate of age-1 fish that survived their first winter. Additionally, we found no apparent seasonal trend in rates of YOY consumption (Figure 3) and number of cannibals (Figure 4) or size selection by cannibals (Figures 5 and 6).

As observed in this study, the annual recruitment of largemouth bass is highly variable (Summerfelt 1975). Largemouth bass males guard nests that may contain as many as

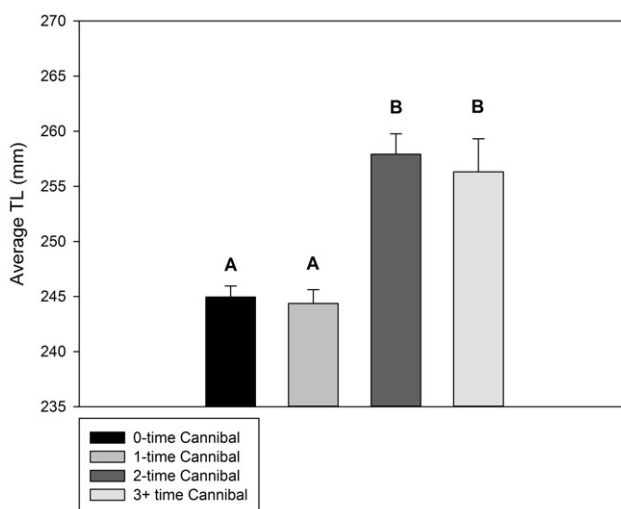


Figure 8. Size (TL) comparisons for recaptured fish that were either non-cannibals, consumed YOY on one occasion, consumed YOY on two occasions, and those that consumed YOY on three or more occasions. Posthoc analysis showed significant differences between groups denoted as 'A' and 'B' between 1984 and 2010 ($H = 53.5$, $p = 0.000$).

2000–7000 fry for up to 5 weeks (Breder 1936; Scott and Crossman 1973; Chew 1974). While this behavior certainly increases the number of eggs and larvae that hatch, there is typically no relationship between hatching success and the number of YOY that survive their first winter (Post et al. 1998; Gwinn and Allen 2010). Post et al. (1998) quantified the impact of cannibalism on recruitment in Paul Lake through bioenergetic modeling based on population estimates for YOY collected between 1993 and 1995. They found that predation on YOY was much more intense during years of high adult and juvenile densities. Contrarily, Purdom et al. (2015) measured annual diet fluctuations of largemouth bass in Paul Lake between 1984 and 2010 using a composite Index of Relative Importance (IRI; George and Hadley 1979) based on seven functional diet groupings. They found that prey IRI values fluctuated irregularly from expected density-dependent patterns. There was no evidence of the predicted density-dependent foraging response on YOY prey as the models had predicted. We also found no evidence of any correlation between the population density and the annual cannibalism on YOY (Figure 9).

We estimated the annual recruitment of age-1 fish by compiling the number of the smallest juveniles (87–125 mm) collected that could not be classified as YOY based on the findings of Post (2003). We did not find a correlation between our estimates of age-1 recruitment and years in which the adult and juvenile population density either increased or declined. It was not the original intent of the study design to collect this size class and apart from efforts to specifically target YOY fish between 1993–1995 (see Johnson and Post 1996; Post et al. 1997, 1998; Post 2003), no specific sampling methodology was employed to increase the likelihood of their capture. This is why our sample size is relatively small (810) compared to the total number of fish collected throughout the study. Nevertheless, our recruitment estimates are mostly in agreement with the mark-recapture findings for two YOY cohorts also collected in Paul Lake with one difference (Post et al. 1997, 1998). This included one of the largest YOY cohorts of largemouth bass ever recorded in 1993. That cohort, however, experienced high mortality (98%) during the winter of 1993–1994 (Post et al. 1997). Our estimate of age-1 recruitment (i.e. YOY survival) was roughly 6% in 1994. Conversely, Post et al. (1997) found that a larger

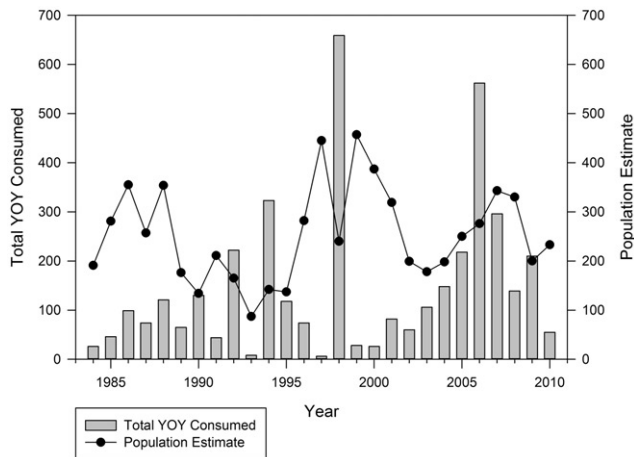


Figure 9. Total cannibalism per year and whole-lake population density estimates between 1984 and 2010.

proportion of the 1994 YOY cohort survived (26%) the winter of 1994–1995. We estimated that there was roughly a 37% increase in the recruitment of age-1 fish in 1995 based on the collection of 206 individuals of that size class. Generally, strong years of recruitment were relatively uncommon with estimates exceeding 10% in only 4 years between 1984 and 2010. Post et al. (1998) found that overwinter mortality was size dependent and that YOY <50–60 mm were unlikely to survive until spring. Additionally, we found that only 3% of consumed YOY over three decades had TL ≥ 70 mm and Post (2003) found around 5% of a single cohort (1994) reached that same size, indicating cannibalism on YOY was intense. Overall, our findings provide additional evidence that the YOY annual mortality is typically quite high in Paul Lake as has been previously recorded (Post et al. 1997, 1998). Yet, we found no direct correlation between age-1 recruitment and changes in the adult and juvenile population density over time.

Furthermore, Post et al. (1998) found that juvenile bass were the most important predators in Paul lake accounting for roughly 90% of all YOY consumed. However, they categorized the adult size class as fish that were ≥ 300 mm in length. We instead relied on Clady (1974) and categorized adults as fish ≥ 230 mm. The average cannibal length of 229 mm (SE ± 1.63) thus sat at the threshold between each size class. Regardless of size, cannibals consumed an average of 4.19 YOY (range 1–105). We did detect subtle, but not statistically significant, differences in the size of YOY prey consumed between the adult and juvenile size class (Figure 5). However, as previously noted, these data were from a smaller subset of analyzed gut contents collected from 62 adult and 32 juvenile fish. It is highly unlikely that the subtle difference in the size of prey consumed between adults and juveniles were in any way related to distinct morphological features such as gape width, especially since there was no significant differences in the size of prey and the gape of a juvenile bass would not typically prevent the consumption of a 15 mm TL YOY versus a 10 mm item. The size of ingested prey consumed by both adults and juveniles appeared to significantly increase across the season (Figure 6), likely reflecting the growth of individual YOY that had survived prior to the point of predation (Figure 7), but the differences could not be recovered post-hoc, once again making interpretation unclear.

The juvenile size class (87–229 mm) was more impacted by dramatic shifts in population density (Table 1). We collected relatively few juveniles compared to the number of adults during years in which the overall population density had significantly declined.

This suggests that adult and juvenile fish may experience differing rates of seasonal mortality. Conversely, we collected many more juveniles than adults during years in which the population was the greatest as younger fish were recruited into the population. This is not surprising as many field and laboratory studies involving teleost fish have found that larger individuals suffer lower rates of mortality than smaller conspecifics (see review by Sogard 1997). Larger individuals (i.e. adults) are less vulnerable to predation and may exhibit enhanced resistance to starvation and are more likely able to tolerate environmental extremes (Sogard 1997).

Temporal variation in population dynamics is reduced by early cannibalism (reviewed by Andersson et al. 2007) and may serve as a 'lifeboat' mechanism that helps the population survive during periods in which food is scarce (Orr et al. 1990; Hastings and Costantino 1991). This may be especially true in Paul Lake, which sits at the northern edge of the species' range. Apart from the very episodic appearance of other fish species, Paul Lake primarily supports a single-species system comprised entirely of largemouth bass. Largemouth bass in Paul Lake are opportunistic cannibals (Hodgson and Kitchell 1987) that largely consume benthic macroinvertebrates and pelagic invertebrates while exhibiting significant inter-annual variations (55%) in their consumption of fish prey (Purdom et al. 2015). Specifically, Hodgson and Hodgson (2000) previously found in Paul Lake over a shorter duration than this study that as YOY cannibalism increased, predation on odonate naiads and *Chaoborus* larvae decreased; odonates are less energetically favorable diet items than YOY (Werner 1979), but are frequently consumed (Hodgson and Kitchell 1987), and largemouth bass often intentionally target *Chaoborus* as prey (Rick et al. 2011). They also found, using bioenergetics modeling, that the proportion of maximum daily consumption was the greatest when YOY consumption was the highest. In many ways, the population in Paul Lake resembles that of the Eurasian perch (*Perca fluviatilis*), another cannibalistic species which is often the only fish encountered in boreal lakes (Persson et al. 2000). These populations, like the one in our study, are characterized by slow-growing individuals due, in part, to high intra- and intercohort competition (Alm 1946, 1952; Sumari 1971; Persson et al. 2000).

Largemouth bass exhibit ontogenetic niche shifts that effectively divide the population into different size classes, or life stages, based on their dietary preferences and habitat use (Nisbet et al. 1989; Osenberg et al. 1992; Olson 1996). Hatchling YOY hover in demersal beds guarded by the male parent (Heidinger 1976) until they reach lengths of roughly 15 mm (Johnson and Post 1996). They then transition into littoral zones seeking shelter from predation while feeding on zooplankton and invertebrate prey (Clady 1974; Keast 1985; Olson et al. 1995). Post et al. (1997) found that large cohorts of YOY in Paul Lake can affect the structure of the food web through intense planktivory and effectively eliminate large-bodied zooplankton by the middle of August. As the cohort ages they transition from feeding on zooplankton to invertebrates and ultimately become more piscivorous typically beginning in their second year of growth (Post et al. 1997; Post 2003). This transition to piscivory with age has the opposite impact on the structure of the food web as small zooplanktivorous YOY are rapidly consumed. Cannibalism on YOY provides a direct energetic benefit to the consumer and helps reduce overall competition for shared resources including large bodied zooplankton and macroinvertebrates (Persson et al. 2000). Intense cannibalism during years in which the adult and juvenile population density is high can eliminate up to 98% of the YOY cohort in as little as four weeks (Post et al. 1998) and minimize the impact of recruitment in the following year (Post et al. 1997).

Foraging theory predicts diet specialization reduces competition for prey and frees resources with different energy yields (Claessen et al. 2000, 2002; Persson et al. 2004). In this manner, cannibalism on YOY may increase the relative profitability of different resources and promote dietary specialization among certain members of the population (Andersson et al. 2007). Schindler et al. (1997) found evidence that individual foraging consistency among bass in Paul Lake was the result of active selection for particular prey types. In our study, we examined the diet records of recaptured adult and juvenile fish to determine if there was a relationship between body size (TL) and cannibalism frequency. Those individuals who were recaptured on two or more occasions with YOY in their stomach contents had significantly greater TL than individual non-cannibals or fish that had ingested YOY on only one sampling occasion (Figure 8). Our findings provide additional evidence that the foraging flexibility of largemouth bass in Paul Lake allows individuals to specialize on subsets of prey resources available to the population (Schindler et al. 1997; Hodgson et al. 2008; Rick et al. 2011). In other populations, largemouth bass that transition to piscivory during their first summer have growth rates approaching two to three times that of their non-cannibalistic conspecifics (Shelton et al. 1979; Olson 1996). In 1994, the few YOY from Paul Lake, the that were able to transition to piscivory during their first year of growth reached nearly 2.5 times the length and over 15 times the mass of the smallest members of their cohort (Post 2003). Post (2003) notes that individuals that transition to, and sustain, piscivory during their first summer potentially maintain a significant size advantage for many years over the other members of their cohort. Without a reliable estimate of the age of these cannibal specialists, it remains unclear if they potentially transitioned to piscivory at an early age and were still relatively young, or if they were simply older fish who survived long enough to ultimately achieve larger body size.

Moreover, cannibalism potentially provides energetic benefits to all surviving members of the population, including cannibals and non-cannibals alike (Claessen et al. 2000, 2002; Persson et al. 2004; Andersson et al. 2007). We therefore predicted that we would be able to detect differences in the growth rate of recaptured individuals collected during years in which the population density and rate of cannibalism differed. Specifically, we expected that fish recaptured during years of low population density when cannibalism was intense would exhibit a greater instantaneous growth rate (G_o) and percent change in length/day than would fish collected during years in which those conditions were reversed. We found no evidence that this was true and intense cannibalism during a particular year was not accompanied by an increase in the growth rate of recaptured individuals. As stated previously, the growth rate of cannibals clearly exceeds that of non-cannibals from the same year's cohort (Shelton et al. 1979; Olson 1996; Post 2003). But here, our results suggest that the indirect energetic benefit that cannibalism provides by increasing the relative profitability of other prey resources not consumed by the YOY cohort may be potentially overstated.

In conclusion, our results suggest that the Paul Lake largemouth bass population was relatively stable over the three decades of observation. Despite intense cannibalism and YOY mortality within the monospecific fish assemblage, the population sustained a modest average annual recruitment rate across the study. Population size did change, but differences in cannibalism within years and between years appeared to have no effect on driving population dynamics. This suggests that cannibalism was an ever-present pressure in the lake, but it likely also offered some benefits to the population, especially considering repeat cannibals were larger individuals. Over the years of observation in Paul Lake, it has been repeatedly noted that the bass were highly opportunistic (Hodgson and Kitchell

1987; Hodgson and Hodgson 2000; Purdom et al. 2015) and adjusted their foraging behavior as higher quality prey became available, even if only temporarily. Furthermore, largemouth bass have been shown to eliminate certain episodic high quality prey from Paul and other nearby lakes (Hodgson and Hodgson 2000). It appeared that seasonally available YOY were an important resource that was routinely exploited, but yet the risk of local extirpation was not observed and did not seem apparent. While our results presented here are strictly a long-term natural history account, they may be of value for largemouth bass fisheries, particularly when studying and/or managing monospecific or simple fish communities in the northern latitudes of the species.

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