Applying a Reservoir Functional-Zone Paradigm to Littoral Bluegills: differences in length and catch frequency?

ABSTRACTReservoirs possess gradients in conditions and resources along the transition from lotic to lentic habitat that may be important to bluegill ecology. The lotic-lentic gradient can be partitioned into three functional zones: the riverine, transitional, and lacustrine zones. We measured catch frequency and length of bluegills (*Lepomis macrochirus*) captured along the periphery of these areas (i.e. in the littoral zone of each functional zone) for four small reservoirs in Southeastern Ohio during the summer months of three years. Catch frequency differed between zones for two reservoirs, but these differences were not repeatable in other years. There was no relationship between reservoir zone and either standard length or catch frequency when the data for all reservoirs were pooled, but we did observe a bimodal length distribution in all reservoirs. A combination of ecological factors including inter and intraspecific competition, predation intensity, management practices, limnology, and assemblage complexity may be mitigating bluegill distribution and abundance in reservoirs that may necessitate mesocosm or whole-reservoir manipulation in order to fully understand.

Nathan Ruhl

Department of Biology, Rowan University, Glassboro NJ 08025

Holly DeAngelis, Abigale M Crosby, and Willem M Roosenburg

Department of Biological Sciences, Ohio University, Athens Ohio 45701

Introduction

Bluegills exhibit ontogenetic habitat shifts that coincide with shifts in foraging behavior in natural lakes. After hatching in the littoral zone, young-of-year migrate to the limnetic zone to feed on zooplankton (Werner, 1969). Once a larger body size has been obtained, the fish return to the littoral zone and feed opportunistically amongst macrophytes. After several years feeding in the littoral zone, larger bluegills shift back to a diet of zooplankton and move freely between the littoral and limnetic zones (Mittelbach, 1981). Shifts in diet and habitat use by bluegill may be a result of a trade-off between maximizing foraging efficiency while minimizing predation risk (Werner and Hall 1988). However, Wildhaber and Lamberson (2004) suggested an alternative hypothesis based on a hierarchical model of trade-offs between prey availability and temperature in lakes. Regardless of the specific cause of the shift in bluegill habitat use (direct selection pressure via predation or indirect pressure from prey/habitat availability), it is an effective life history strategy (reviewed by Werner and Peacor, 2003).

The successfulness of habitat switching as a life history strategy for bluegills may depend on a number of factors. For instance, basin morphometry may lead to differential recruitment success of bluegills between natural lakes; maximum depth, percent littoral area (Tomcko and Pierce, 2001), and lake surface area (Tomcko and Pierce, 2005) have all been linked to recruitment success. Habitat features such as the availability of woody debris (Newbrey et al, 2005), and native macrophytes (Theel and Dibble, 2008) in the littoral zone are positively associated with bluegills. Another important factor is the availability of zooplankton (Garvey and Stein, 1998); in lakes with low productivity or high turbidity, zooplankton abundance may be negatively impacted by low epilimnetic phytoplankton abundance that results in reduced bluegill recruitment (Stein et al, 1995). High abiotic turbidity in the photic zone is normally driven by physical processes such as wind mixing and flooding but can also be influenced by sympatric species (e.g. gizzard shad; Vanni et al, 2005) resulting in both direct and indirect density-dependent effects on bluegill recruitment via alteration in prey availability and/or capture success (Aday et al, 2003; Shoup et al, 2007). Indeed, protracted spawning by bluegills (Garvey et al, 2002) may be an adaptation to offset density-dependent effects caused by competition for prey (Partirdge and DeVries 1999, Michaletz, 2006; but see Leonard et al, 2010).

Within reservoirs, there are gradients in the relative area of littoral vs. limnetic habitat (Thornton, 1990), zooplankton community composition (Bernot et al, 2004), and a suite of environmental variables including turbidity (Thornton, 1990) and available nutrients (Kennedy and Walker, 1990) along the lotic-lentic transition. Reservoirs can be divided into three functional zones based on these asymmetries (Figure 1): the fluvial zone is the shallow un-stratified portion that is heavily influenced by flooding and where well-mixed epilimnetic water is in direct contact with sediments, the transitional zone is weakly stratified and less influenced by flooding or sediment resuspension, and the lacustrine zone is the stably stratified lake-like area (adapted from Kimmel et al, 1990).

Interpreting the ecological dynamics of reservoirs against the paradigm of functional zones along the lotic-lentic transition has been regularly applied to organisms that are at the whim of hydrologic conditions (reviewed by Ruhl, 2013a), but to our knowledge has not been explicitly assessed in relation to more motile species such as fish. Additionally, the functional-zonation scheme for reservoirs has typically been used by researchers working in open water rather than along the shoreline (littoral zone), despite the fact that differences in the mixing regime in open-water may directly influence factors such as nutrient availability along the periphery. Because bluegill ecology is intimately linked to the conditions and resources in the limnetic as well as littoral zones, the functional-zone paradigm may be particularly relevant to them and yield insight into broad-scale differences in their ecology within reservoirs (i.e. both along the lotic-lentic gradient and between the littoral and limnetic zones). Specifically, we predicted that size and catch frequency may vary between functional zones because of differences that affect bluegill recruitment (i.e. their suitability for growth and reproduction; see above). In order to assess bluegills relative to the reservoir zones along the lotic-lentic transition, we sampled the littoral zone throughout four different reservoirs (in multiple years in some cases) during the period when stable thermal stratification is normally strongest (July and August) and therefore differences between functional zones may be at their peak.

Methods

Study sites

We trapped Dow Lake, Lake Hope, Lake Snowden and Fox Lake; four reservoirs located in close proximity to one another in the un-glaciated hills of Southeastern Ohio and managed by units of the Ohio Department of Natural Resources (Figure 2, Table 1). Dow Lake (Stroud's Run State Park) is used primarily for recreation, but also to mitigate flooding of the Hocking River downstream of Athens, Ohio. This reservoir was initially filled in 1960 and the watershed is composed of minimally disturbed hills, woodland, and open fields. Throughout the reservoir, the littoral zone was modified via the felling of shoreline trees and addition of brush piles to coves in 2000-2001 (Greenlee, per comm.).

Lake Snowden was created in 1970. The reservoir previously supplied drinking water to the surrounding community, but is currently used for flood control, hatchery water supply, and recreational activities. The watershed consists of rolling hills, agricultural fields, and woodlots while the shoreline habitat includes submerged trees, overhanging brush and abundant submerged macrophytes.

Fox Lake was originally filled in 1968 and the watershed is composed of rolling hills, agricultural fields and woodlots. High sedimentation rates in the riverine zone have resulted in poor angler access to the reservoir and, consequently, submerged macrophytes were removed in 1994-95 to increase flow and accessibility in the riverine zone (Greenlee, per comm.). These efforts were not successful in improving angler access and dredging to remove sediment has been deemed impractical.

Lastly, Lake Hope is located within the Zaleski State Forest and was initially filled in 1937. The watershed is composed of mature second growth forest scattered with abandoned pit and shaft coal mines. The reservoir has abundant invasive emergent macrophytes (primarily *Nymphaea odorata*) mixed with a variety of other emergent and submerged macrophytes around the periphery.

Bluegills are not regularly stocked into any of the reservoirs (Table 1). Rainbow trout (*Oncorhynchus mykiss*, mean length 303mm, 2001-2011) are stocked into Dow Lake every April. All four reservoirs are stocked yearly or in alternating years with channel catfish (*Ictalurus punctatus*, mean 221mm) in the fall. Lakes Snowden and Hope are stocked with saugeye (*Sander canadensis* x *Sander vitreus*, mean 31.5mm) every year in the spring. Fish are normally stocked into the reservoirs in close proximity to the boat launch (Greenlee, per comm.), meaning that stocked fish are introduced into the riverine zone at Dow Lake and Fox Lake, the transitional zone at Lake Snowden, and the lacustrine zone at Lake Hope.

Sampling regime

The reservoirs were sampled over the course of three years, but only Dow Lake and Lake Hope were repeatedly sampled (Table 2). Sampling occurred during July and August in all years, but the number of weeks during which trapping occurred varied by year. All trapping was conducted using a randomized block design both within and between reservoirs, thereby minimizing the likelihood of a temporal effect between reservoirs or reservoir zones within a given year. Sampling methods were in accordance with Ohio University IACUC protocols and Ohio Department of Natural Resources Permit #464.

At each trapping site, pairs of oval traps (Promar 'large' 81 x 50 x 30cm`(1 cm mesh size and 12cm minimum tunnel diameter) and 'extra-large' 91 x 62 x 50cm (2.5cm mesh and 15cm tunnel diameter)) were positioned about 2m from one another with trap entrances positioned parallel with the shoreline. Each site used two 'large traps' in 2006; in 2007 and 2008 each site had one 'large' and one 'extra-large' trap. 'Extra-large' traps were introduced in 2007 and 2008 to ensure that we were not excluding larger bluegills (and incidentally to validate the 2006 size data). Trapping sites were located at approximately equal intervals around the periphery (littoral zone) of each reservoir. We baited each trap with commercially available dip bait (Premo brand 'original super-sticky dip bait') hung inside the trap in a cheesecloth bag. We checked traps every 24 hours for five days, measured the standard length of each fish and then released them at the point of capture.

Analysis

Determination of the extent of the transitional zone (and therefore the corresponding size of the riverine and lacustrine zones) was done *a posteriori* for each reservoir and each year. For our purposes, the transitional zone is defined as the area of the reservoir where the extent of thermal stratification fluctuated due to weather conditions (wind and flooding). Therefore, the transitional zone begins at the point when a well-mixed epilimnion and a metalimnion are present outside of the thalweg (if present) and continues until underflows terminate into interflows through the metalimnion (Figure 1).

Attempts to normalize length and catch frequency (the total number of fish caught over a five day period for each site) data were unsuccessful in most cases. Therefore, comparisons between reservoir zones (i.e. within each reservoir) were conducted using Kruskal-Wallis tests and *a priori* Mann-Whitney U-tests. The same tests were used when comparing catch frequency between reservoir zones for all reservoirs combined, but one-way ANOVA with post-hoc Tukey tests were employed to compare the standard length between zones for all reservoirs combined. Although the length data was not normal, ANOVA is robust for non-parametric data at sample sizes greater than 100. When comparing the catch frequency of small vs. large bluegills (see results) between reservoir zones for the pooled data (all reservoirs combined), a two sample Kolmogorov-Smirnov test was conducted. All statistics were performed using SPSS 12.0 and the raw data is available in the supplemental materials.

Results

Standard length

Standard length only varied by reservoir zone for Dow Lake in 2006. In that case, bluegills caught in the transitional zone were smaller than those caught in the other zones (riverine: Mann-Whitney, U=412, p=0.019; lacustrine: U=431.5, p=0.004), but this result was not seen in 2007 (Figure 3). When the length data from all reservoirs was combined, there were no differences among zones (one-way ANOVA, $F_{(2, 822)}=0.053$, p=0.921).

Catch frequency

There was no difference in the catch frequency of bluegills between reservoir zones for any of the reservoirs (Table 2). Catch frequency did not vary between reservoir zones when the data from all reservoirs was pooled either (Kruskal-Wallis, $\chi^2=1.094$, p=0.579). Because the distribution of lengths was bimodal for all reservoirs in all years, the dataset was bifurcated at the saddle of the distribution (>/< 8.5 cm, Figure 4) and we asked if the number of small or large bluegills varied over reservoir zone for each reservoir. Only Lake Hope showed any differences in this secondary analysis: small bluegills were encountered more often in the transitional zone than in the fluvial zone in 2008 (Mann-Whitney, U=357, p = 0.019; Figure 5), but this result was not observed in the previous year. When the bifurcated data were combined for all reservoirs, there was no difference in the catch frequency of small or large bluegills between zones (Kruskal-Wallis, small: $\chi^2=2.285$, p=0.319; large: $\chi^2=.406$, p=0.816). Additionally, there was no relationship between the catch frequency of small vs. large bluegills between reservoir zone (Kolmogorov-Smirnov, Z=1.083, p=0.192).

Discussion

Bluegill populations are influenced by a variety of factors including both abiotic factors such as turbidity (Stein et al, 1995) or temperature (Wilhaber and Lamberson, 2004) and biotic factors such as prey availability (Garvey and Stein, 1998; Hoxmeier et al, 2009) or predators (Werner and Hall, 1988); these three factors all vary dramatically between reservoir zones as a simple function of stratification regime (as well as other factors such as nutrient loading, water retention time, etc). However, few differences in bluegills between reservoir zones were observed in our study. Size of bluegills differed between zones at Dow Lake in 2006, but this result was not repeatable in 2007. Similarly, small bluegills were caught more frequently in the transitional zone at Lake Hope in 2008, but not in 2007. When the data from all reservoirs was pooled, there were no differences in either size or catch frequency between reservoir zones, suggesting that habitat partitioning may be based on different criteria in reservoirs (Gelwick and Matthews, 1990; Eggleton et al, 2005) than has previously been described for natural lakes (e.g. Werner et al, 1977).

The lack of repeatability in our findings between years may be indicative of the true nature of reservoirs as a habitat for bluegills. With respect to bluegills, resources and conditions within a reservoir may be dependent on prevailing weather patterns (Lienesch and Matthews, 2000; but see Edwards et al 2007), inputs from the watershed (Gido et al, 2002; Vanni et al, 2005) and (in some cases) the presence of certain species (e.g. gizzard shad; Vanni et al, 2005). All of these variables can fluctuate dramatically between years and cause shifts in prey availability (Betsill and Vandenavyle, 1994) and predation intensity (Jackson and Noble, 2000). Additionally, due to reservoirs being artificial and managed waterbodies, the effect of water level changes on habitat availability/suitability (Collingsworth and Kohler, 2010) and stocking of competitors (Leonard et al, 2010) and/or predators may vary from year to year. Therefore, while size and catch frequency of bluegills may differ by reservoir zone at times (as we observed at Dow in 2006 and Hope in 2008), they are likely influenced by other factors as well, which may have disrupted our ability to consistently detect differences among zones.

Bluegill spawning behavior may also influence the detectability of differences in length and catch frequency between reservoir zones. Bluegill spawning is condition-dependent for males (males in better physical condition spawn first; Cargnelli and Neff, 2006), which results in protracted spawning (spawning over an extended period). Given the differences in prey availability between reservoir zones (Betsill and Vandenavyle, 1994), protracted spawning may be more prevalent in reservoirs than in lakes and could cause behavioral plasticity in habitat-use that is difficult to detect using standard techniques (e.g. trapping, netting, or electro-shocking). That is, if bluegill spawning occurs over a wider range of times in reservoirs, population-wide shifts in habitat use would be similarly spread over a longer time-frame and differences between zones, which may be important to bluegills, may also be difficult to detect. This is supported by Jolley et al (2009), who found that the timing of spawning in bluegills varied between nearby reservoirs and between years in the same reservoirs.

The size structure of the bluegills we caught through trapping (all reservoirs combined) was bimodal. While mesh size excludes smaller fish and larger individuals are typically rare (resulting in tails of the distribution), it was interesting that we saw a distinct saddle (low abundance) of fish at about 8.5cm. Bluegills <10 cm (except planktivorous larvae) are normally found in the littoral zone of lakes because this area provides the greatest protection from predation (Werner and Hall, 1979). It may be that in our study, bluegills move away from the shoreline reservoir-wide at a much smaller size in reservoirs then in natural lakes, but we feel this is unlikely given the differences in 'offshore' conditions and resources between reservoir zones. Likewise, it is possible that the saddle of the distribution represents two different age classes, but this is also unlikely given the variation in growth rates observed in bluegills between reservoirs (Jackson et al, 2008) and their protracted spawning behavior. More likely, the saddle is a result of size-selective predation by largemouth bass (Olson, 1996) or other piscivores such as saugeye. Because these piscivores are gape limited, bluegills over about 10 cm (Werner and Hall, 1979) are at lower risk of predation than smaller bluegills (Santucci and Wahl, 2003). Therefore, the saddle may represent the point at which age-specific mortality of bluegill caused by predation (Mittelbach and Persson, 1998) starts to decline in Southeastern Ohio reservoirs.

Lastly, another factor that may have contributed to our results is that our methodology did not detect temporal variation within a reservoir. Because trapping occurred over the course of a few weeks for each reservoir, differences in catch frequency or size between zones as a result of behavioral plasticity during ontogeny may be diluted. However, Gelwick and Matthews (1990) suggest that there is little temporal variation in littoral fish assemblages of reservoirs relative to lakes because these assemblages are 'evolutionarily short-lived'; because a given reservoir has not existed long in evolutionary time, fish assemblages may not exhibit the same patterns seen in natural lakes which have existed for many years. Our results seem to support this conclusion given that we only saw differences in the oldest of the reservoirs we sampled. Similarly, anthropogenic factors such as intensive stocking (Gelwick and Matthews, 1990) or the maintenance of a community dominated by a small number of species (Eggleton et al, 2005) may contribute to a decrease in temporal variation in habitat-use in reservoirs.

In this study, bluegills usually did not differ in size or catch frequency between reservoir zones in four Southeastern Ohio reservoirs. This result, while unexpected due to the broad differences in habitat characteristics between reservoir zones, may be caused by a combination of factors including prey availability relative to predation intensity in reservoirs, management practices, limnology, and assemblage complexity. Mesocosm and whole-reservoir manipulations may be able to tease apart the relative importance of these factors and the lotic-lentic transition in future studies. For instance, prey availability, predation intensity, and assemblage complexity can be easily manipulated by changing the stocking regime of a given reservoir. Similarly, the impact of limnological variables in combination with predation intensity or prey availability is easily manipulated using mesocosms. While the reservoir functional-zone paradigm appears to work for some species inhabiting the littoral zone of Southeastern Ohio reservoirs (Ruhl, 2013b), it does not appear to be an appropriate management tool for littoral bluegills (i.e. bluegills targeted by anglers). However, the functional-zone paradigm may yet be a useful tool in understanding bluegill ecology in the limnetic zone, and should be assessed in that context.

Acknowledgments

We wish to thank all of the undergraduate assistants who participated in sampling, the members of the Roosenburg lab for their helpful suggestions, and Drs. Warren JS Currie and K Cuddington for their assistance. Two anonymous reviewers provided comments that improved an earlier version of this manuscript.

Bibliography

Aday DD, Hoxmeier JH, Wahl DH. 2003. Direct and indirect effects of gizzard shad o bluegill growth and population size structure. *Transactions of the Americans Fisheries Society.* 132:47-56.

Bernot RJ, Dodds WK, Quist MC, and Guy CS. 2004. Spatial and temporal variability of zooplankton in a great plains reservoir. *Hydrobologia*, 525:1-3, 101-112.

Betsill RK and Vandenavyle MJ. 1994. Spatial heterogeneity of reservoir zooplankton – a matter of timing. *Hydrobiologia*, 277:1, 63-70.

Cargnelli LM and Neff BD. 2006. Condition-dependent nesting in bluegill sunfish *Lepomis macrochirus*. *Journal of Animal Ecology*, 75:3, 627-633.

Collingsworth PD and Kohler CC. 2010. Abundance and habitat use of juvenile sunfish among different macrophyte stands. *Lake and Reservoir Management*, 26:1, 35-42.

Edwards KR, Phelps QE, Graeb BDS, and Willis DW. 2007. Asynchronous bluegill recruitment in four South Dakota impoundments. *Journal of Freshwater Ecology*, 22:1, 19-22.

Eggleton MA, Ramirez R, Hargrace CW, Gido KB, Masoner JR, Schnell GD, and Matthews WJ. 2005. Predictability of littoral-zone fish communities through ontogeny in Lake Texoma, Oklahoma-Texas, USA. *Environmental Biology of Fishes*, 73:1, 21-36.

Garvey JE and Stein RA. 1998. Competition between larval fishes in reservoirs: The role of relative timing of appearance. *Transactions of the American Fisheries Society*, 127:6, 1021-1039.

Garvey JE, Herra TP, and Leggett WC. 2002. Protracted reproduction in sunfish: The temporal dimension in fish recruitment revisited. *Ecological Applications*, 12:1, 194-205.

Gelwick FP and Matthews WJ. 1990. Temporal and spatial patterns in the littoral-zone fish assemblages of a reservoir (Lake Texoma, Oklahoma-Texas, USA. *Environmental Biology of Fishes*, 27:2, 107-120.

Gido KB, Hargrave CW, Matthews WJ, Schnell GD, Pogue DW and Sewell GW. 2002. Structure of littoral-zone fish communities in relation to habitat, physical, and chemical gradients in a southern reservoir. *Environmental Biology of Fishes*, 63:3, 253-263.

Greenlee, M. Personal Communication. Southeastern Ohio Division of Natural Resources (District 4) Biologist, Athens, Oh.

Hoxmeier JH, Aday DD, and Wahl DH. 2009. Examining interpopulation variation in bluegill growth rates and size structure: effects of harvest, maturation, and environmental variables. *Transactions of the American Fisheries Society*, 138:2, 423-432.

Jackson JR and Noble RL. 2000. Relationships between annual variations in reservoir conditions and age-0 largemouth bass year-class strength. *Transactions of the American Fisheries Society*, 129:3, 699-715.

Jackson ZJ, Quist MC, and Larscheid JG. 2008. Growth standards for nine North American fish species. *Fisheries Management and Ecology*, 15:2, 107-118.

Jolley JC, Edwards KR, and Willis DW. 2009. Bluegill (*Lepomis macrochirus*) apawning periodicity and hatching duration in the Northern great plains, USA. *Journal of Freshwater Ecology*, 24:1, 29-38.

Kennedy RH and Walker WW. 1990. Reservoir Nutrient Dynamics. In K. W. Thornton, B. L. Kimmel, and F. E. Payne (eds.), Reservoir Limnology: Ecological Perspectives, pp. 109-131. John Wiley and Sons, New York, NY

Kimmel B. L., O. T. Lind, and L. J. Paulson. 1990. Reservoir primary production. In K. W. Thornton, B. L. Kimmel, and F. E. Payne (eds.), Reservoir Limnology: Ecological Perspectives, pp. 133-194. John Wiley and Sons, New York, NY

Leonard DM, Devries DR, and Wright RA. 2010. Investigating Interactions between Channel Catfish and Other Sport Fishes in Small Impoundments. *North American Journal of Fisheries Management,* 30:3, 732-741

Lienesch PW and Matthews MJ. 2000. Daily fish and zooplankton abundances in the littoral zone of Lake Texoma, Oklahoma-Texas, in relation to abiotic variables. *Environmental Biology of Fishes*, 59:3, 271-283.

Michaletz PH. 2006. Prey resource use by bluegill and channel catfish in small impoundments. *Fisheries Management and Ecology.* 13, 347-354.

Mittelbach GG. 1981. Foraging efficiency and body size – a study of optimal diet and habitat use by bluegills. *Ecology*, 62:5, 1370-1386.

Mittelbach GG and Persson L. 1998. The ontogeny of piscivory and its ecological consequences. *Canadian Journal of Fisheries and Aquatic Sciences*, 55:6, 1454-1465.

Newbrey MG, Bozek MA, Jennings MJ, and Cook JE. 2005. Branching complexity and morphological characteristics of coarse woody structure as lacustrine fish habitat. *Canadian Journal of Fisheries and Aquatic Sciences*, 62:9, 2110-2123.

Olson MH. 1996. Predator-prey interactions in size-structured fish communities: Implications of prey growth. *Oecologia*, 108:4, 757-763.

Partridge DG and Devries DR. 1999. Regulation of growth and mortality in larval bluegills: implications for juvenile recruitment. *Transactions of the American Fisheries Society*, 128:4, 625-638.

Ruhl N. 2013a. The lotic-lentic gradient in reservoirs and estuaries. In: Ruhl N, The lotic-lentic gradient in reservoirs and estuaries, Ohio University Dissertation.

Ruhl N. 2013b. Spatial, temporal, and sex-dependent differences in eastern musk turtle (*Sternotherus odoratus*) size and catch frequency in a Southeastern Ohio reservoir. In: Ruhl N, The lotic-lentic gradient in reservoirs and estuaries, Ohio University Dissertation.

Santucci VJ and Wahl DH. 2003. The effects of growth, predation, and first-winter mortality on recruitment of bluegill cohorts. *Transactions of the American Fisheries Society*, 132:2, 346-360.

Shoup DE, Callahan SP, Wahl DH, Peirce CL. 2007. Size-specific growth of bluegill, largemouth bass and channel catfish in relation to prey availability and limnological variables. *Journal of Fish Biology.* 70: 21-34.

Stein RA, DeVries DR, and Dettmers JM. 1995. Food-web regulation by a planktivore: Exploring the generality of the trophic cascade hypothesis. *Canadian Journal of Fisheries and Aquatic Sciences*, 52:11, 2518-2526.

Theel HJ and Dibble ED. 2008. An experimental simulation of exotic aquatic macrophyte invasion and its influence on foraging behavior of bluegill. *Journal of Freshwater Ecology*, 23:1, 79-89.

Thornton K. W. 1990. Sedimentary processes. In K. W. Thornton, B. L. Kimmel, and F. E. Payne (eds.), Reservoir Limnology: Ecological Perspectives, pp. 43-70. John Wiley and Sons, New York, NY

Tomcko CM and Pierce RB. 2001. The relationship of bluegill growth, lake morphometry, and water quality in Minnesota. *Transactions of the American Fisheries Society*, 130:2, 317-321.

Tomcko CM and Pierce RB. 2005. Bluegill recruitment, growth, population size structure, and associated factors in Minnesota Lakes. *North American Journal of Fisheries Management.* 25: 171-179.

Vanni MJ, Arend KK, Bremigan MT, Bunnell DB, Garvey JE, Gonzalez MJ, Renwick WH, Soranno PA, and Stein RA. 2005. Linking landscapes and food webs: Effects of omnivorous fish and watersheds on reservoir ecosystems. *Bioscience*, 55:2, 155-167.

Werner RG. 1969. Ecology of limnetic bluegill (*Lepomis macrochirus*) fry in Crane Lake Indiana. *American Midland Naturalist*, 81:1, 164-181.

Werner EE, Hall DJ, Laughlin DR, Wagner DJ, Wilsmann LA, and Funk FC. 1977. Habitat partitioning in a freshwater fish community. *Journal of the Fisheries Research Board of Canada,* 43:3, 360-370.

Werner EE and Hall DJ. 1979. Foraging efficiency and habitat switching in competing sunfishes. *Ecological Society of America,* 60:2, 256-264.

Werner EE and Hall DJ. 1988. Ontogenetic habitat shifts in bluegill: The foraging rate-predation risk trade-off. *Ecological Society of America,* 69:5, 1352-1366.

Werner EE and Peacor SD. 2003. A review of trait-mediated indirect interactions in ecological communities. *Ecology*, 84:5, 1083-1100.

Wildhaber ML and Lamberson PJ. 2004. Importance of the habitat choice behavior assumed when modeling the effects of food and temperature on fish populations. *Ecological Modeling.* 175: 395-409.

Tables

Table 1

Basin Morphometrics, Fill Date, and Date of last Bluegill Stocking for Each Reservoir

Variable	Dow	Fox	Hope	Snowden
Catchment Area (km2)	18.90	10.36	25.64	9.78
Surface Area (km2)	0.67	0.23	0.48	0.65
Maximum Depth (m)	9.5	6.0	6.5	10.0
Mean Depth (m)	1.62	1.28	1.31	2.45
Volume (m3)	1085069	294975	630744	1590558
Shoreline Length (km)	11.27	3.86	9.18	11.91
Shoreline Development	5.49	3.21	5.29	5.89
Maximum Fetch (km)	2.00	0.71	1.07	2.87
Fill Date	*1960*	*1968*	*1939*	*1970*
Last Stocked with Bluegill	*1972*	*N/A*	*1979*	*1970*

Table 2

The Number of Sites in Each Functional Zone of Each Reservoir with Summary Statistics for the Number of Bluegills Caught and their Lengths

Site/Year	Zone	#Sites	Abundance	Mean Catch Frequency	Mean Length (cm)
Dow 2006	Riverine	4	57	14.25	9.45
	Transitional	4	22	5.50	7.69
	Lacustrine	8	67	8.38	10.05
Fox 2006	Riverine	5	72	14.40	8.34
	Transitional	2	19	9.50	7.30
	Lacustrine	2	27	13.50	6.83
Dow 2007	Riverine	17	104	6.12	7.89
	Transitional	11	103	9.36	8.00
	Lacustrine	12	92	7.67	8.11
Hope 2007	Riverine	4	31	7.75	7.17
	Transitional	5	47	9.40	7.73
	Lacustrine	6	60	10.00	7.67
Snowden 2007	Riverine	3	25	8.33	8.62
	Transitional	6	59	9.83	9.60
	Lacustrine	7	40	5.71	8.13
Hope 2008	Riverine	4	19	4.75	4.75
	Transitional	6	47	7.83	7.83
	Lacustrine	10	43	4.30	4.60

Note: raw data was used for statistical analysis (not the means presented here).

Table 3

Results of a Kruskal-Wallis Analysis of Catch Frequency between Reservoir Zones for Each Reservoir and Year

Lake	Year	χ^2	P
Fox	2006	2.881	0.237
Dow	2006	5.094	0.078
Dow	2007	0.550	0.760
Snowden	2007	0.793	0.673
Hope	2007	0.812	0.666
Hope	2008	1.832	0.400

Figure 1

Diagram of vertical and horizontal zonation in a stereotypical reservoir

The curve ending in 4^0C represents a stereotypical summer thermocline in a deep reservoir.

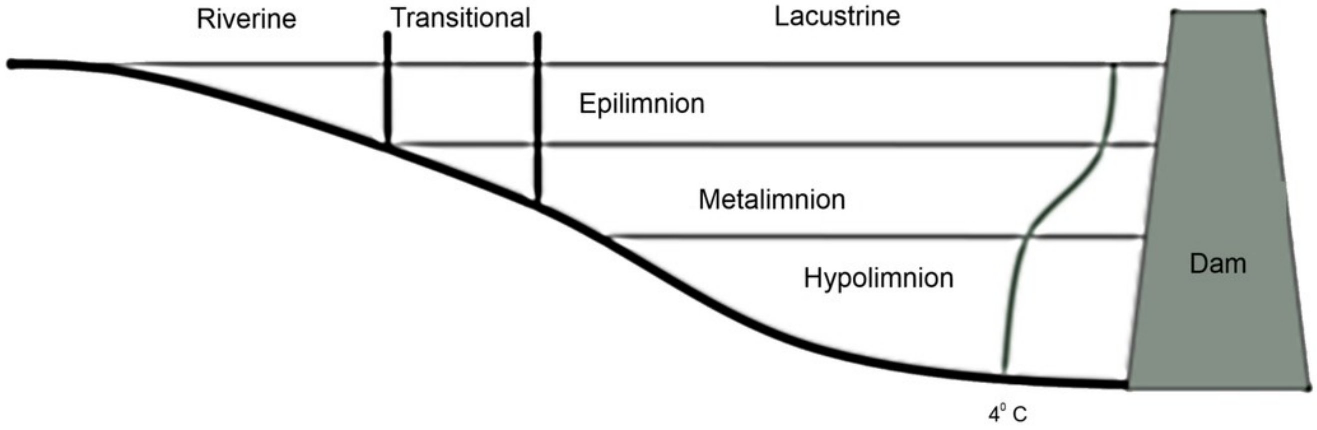

Figure 2

County map of Ohio highlighting the counties where trapping occurred (gray shading; Vinton and Athens) and location of the reservoirs (asterisks)

The bold line indicates the extent of glaciation.

Figure 3

Standard length between zones at Dow Lake in 2006 and 2007.

Bluegills caught in the transitional zone in 2006 were significantly smaller than those caught in the fluvial (Mann-Whitney, U=412, p=0.019) or lacustrine (U=431.500, p=0.004) zones, but this result was not observed in 2007.

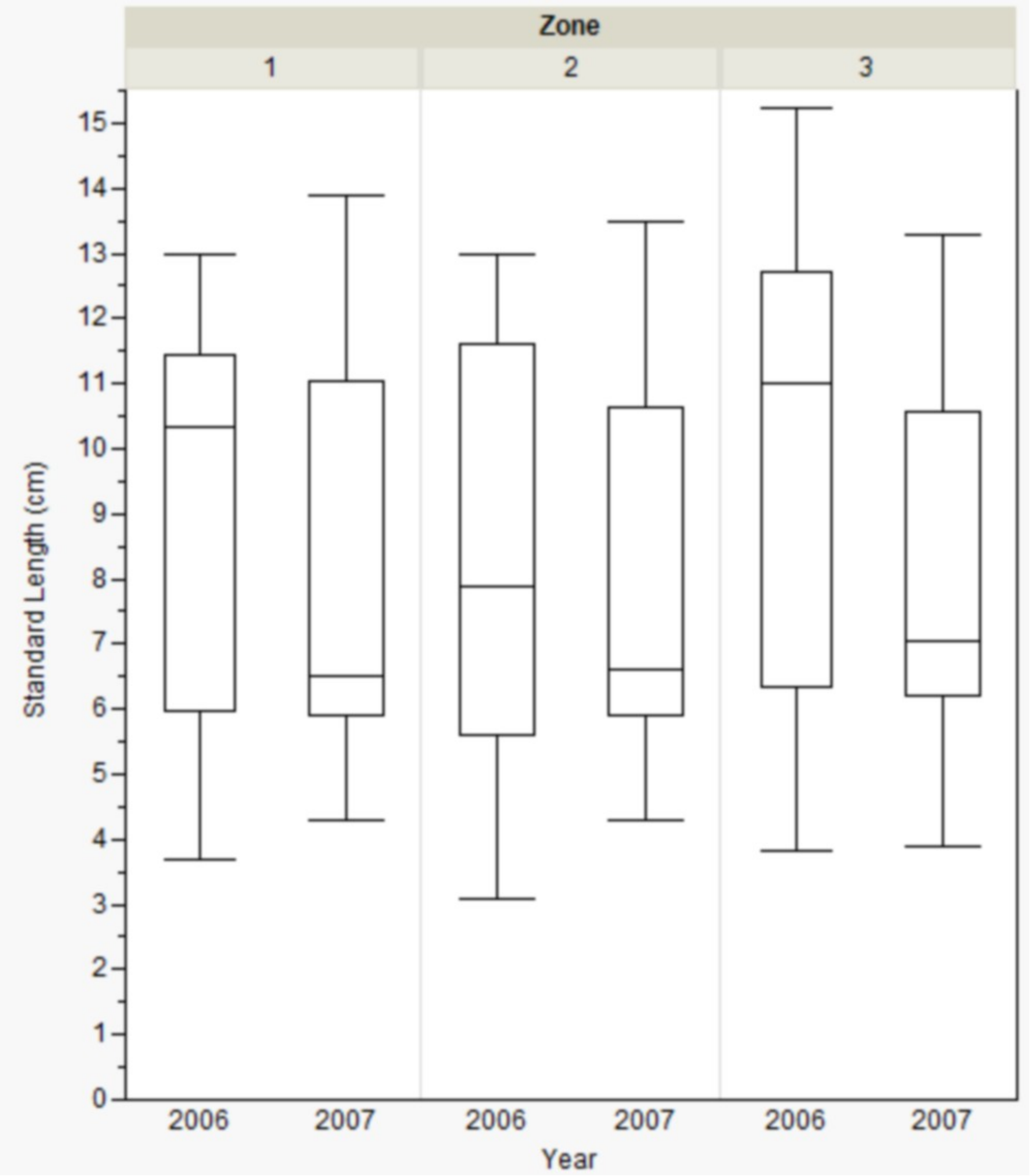
Zone
1
2
3
Standard Length (cm)
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
2006
2007
2006
2007
2006
2007
Year

Figure 4

Histogram of bluegill lengths for all reservoirs combined.

The dashed line indicates the saddle in the distribution at 8.5cm where the data was bifurcated into “small” and “large”.

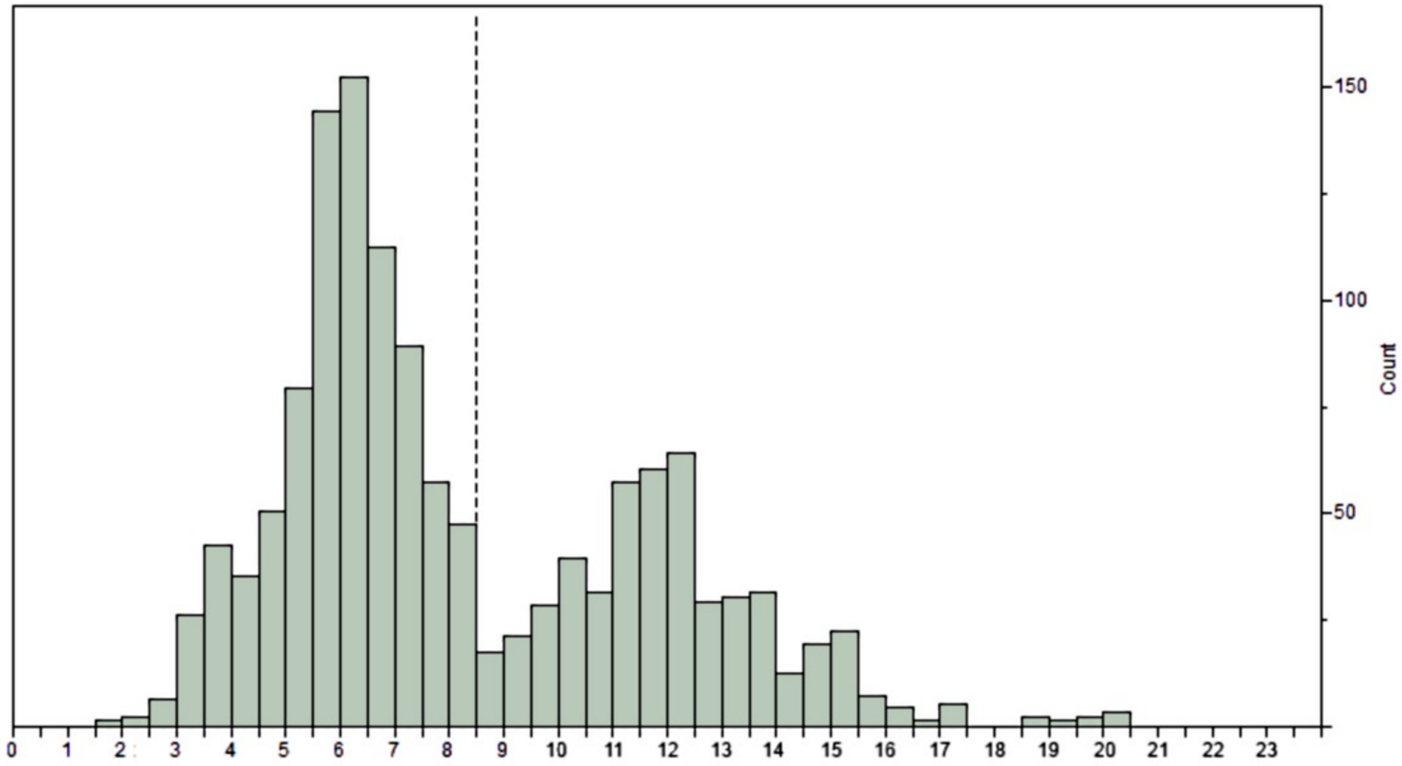

Figure 5

Catch frequency of small bluegills between zones in 2007 and 2008 at Lake Hope.

Catch frequency in the riverine zone was significantly lower than in the transitional zone in 2008 (Mann-Whitney, U=357, p = 0.019), but there were no significant difference between zones in 2007.