Answering Growing Questions of Bluegill's Past – Connecting Changing Body Size to 69 Years
of Environmental Changes

by

Elise Grabda

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Thesis Committee:

Assistant Professor Karen Alofs, Chair

Dr. James Breck

Dr. Kevin Wehrly

Abstract

The differential impacts of climate and anthropogenic stressors on body size and growth are trends of interest for many ecologists studying climate change impacts. These stressors are known to be co-occuring in nature, so untangling the response of body size from one or the other causes is difficult to do without long-term datasets, which are often difficult to access. Recent digitization efforts have now opened the door to new analysis possibilities by providing historical growth data from 1950 to 2019 at 1069 inland lakes in Michigan. I combined historical data with data from recent monitoring efforts to examine changes in mean bluegill length at age. In this study I find juvenile bluegill (*Lepomis macrochirus*) ages one to four have experienced losses in mean body length, while mature adults ages six to eight have seen gains in body size over the same time period. Using Boosted Regression Tree models, I was able to delineate trends in growth that could be attributed to increasing temperatures and length of growing seasons, and morphological characteristics of the lakes, while also accounting for the impacts of other stressors such as land-cover changes, increasing human populations, and assemblage changes at the same time. These models explain between 22% and 61% of deviance in bluegill growth.

Acknowledgements

Beyond the incredible help of my thesis committee, there were many others instrumental in assisting me with this thesis. First among those is Dr. Katelyn King, who's technical and coding knowledge helped to guide me in the early stages of thesis development. Dr. Justin Schell, also assisted with early data wrangling, and coding suggestions. Both people, along with members of my advisory committee collaborated with another team of researchers and the public to digitize and amass the historical data used in this study. Special thanks to Calla Beers and the rest of the Zooniverse team.

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Introduction |

Body size is an important metric which mediates both ecological and physiological processes of animals (Peters, 1983). The most frequent measure of an organism, body size is used to understand change occurring in a variety of taxa and as a comparative metric. Organism fecundity, metabolic rate, dispersal ability, and other core physiological and ecological processes scale with body size and temperature (Ahti et al., 2020; Brown et al., 2004; Hantak et al., 2021; Roy et al., 2003; Rypel, 2014; Weeks et al., 2020). The factors which cause growth to change are multi-faceted and can be indicative of changes to habitat condition.

With climate change increasing environmental temperatures across a range of habitats, we have already seen evidence that body size is decreasing in many species (Sheridan & Bickford, 2011). For example, bird tarsals are shrinking across species as climatic temperatures increase, and the response by many other taxa has been a similar shift to smaller body sizes(Roy et al., 2003; Sheridan & Bickford, 2011; Weeks et al., 2020). Similar decreasing body size can be seen in the fossil record during warming periods of the earth's history. As the climate continues to warm, and thermal tolerances are increasingly exceeded, taxa may be incentivized to spend less time foraging and more time seeking or staying in refuge which limits energy available for growth (Sheridan & Bickford, 2011). A common measure of temperature is the Degree Day (DD), or Growing Degree Day (GDD), which is an integration of the temperature optimal for growth and the length of the growing season (Vøllestad et al., 2022). Although, increasing temperatures are not solely responsible for changes in growth.

Other habitat factors also play a role in determining animal body size (Faurby & Araújo, 2017; Hantak et al., 2021). Preferential harvesting or predation of the largest individuals in communities exerts selective forces to decrease size; and losses in biodiversity reduce food and

nutrient availability that limit growth (Ahti et al., 2020; Rypel, 2014). Land use and land cover development can also dramatically change hydrologic patterns, increasing runoff and nutrient flow to water bodies, and increasing biologically available energy available in inland lakes (Quesada et al., 2017; Zhu & Li, 2014). The other habitat factors do not act independently of climactic stressors but co-occur and potentially interact with one another (Hantak et al., 2021; Lynch et al., 2016). With co-occuring stressors the degree to which changes in the environment impact changes in growth is obscured (Faurby & Araújo, 2017).

Work to understand connections between macroecological patterns in size, the underlying process of growth, and environmental condition has historically focused terrestrial vertebrates and there is a need to understand these patterns in aquatic taxa so we can understand how climate change has and will impact populations (Rypel, 2014). Ectothermic organisms, such as insects, reptiles, and fishes, are especially reliant on thermal-ecological conditions to control their metabolism, and subsequently body size and rate of growth. Increasing temperatures lead to decreases in body size unless the organism compensates with more food intake (Sheridan & Bickford, 2011). Aquatic ectotherms rely on more than temperature to grow, characteristics of the aquatic and surrounding terrestrial environment they reside in also limits growth capacity.

In this study I focus on somatic body size in Bluegill (*Lepomis macrochirus*), due to the species' ubiquity and recorded sensitivity to environmental gradients (Tomcko & Pierce, 2001, 2005). Bluegill body size is correlated with age, habitat preference, and population density. As bluegill mature, they undergo developmental shifts in habitat choice (Werner & Hall, 1988). Juveniles stay in littoral habitats in inland lakes which provide refuge from predators given there is vegetative cover. As bluegill grow with age, they become large enough to avoid predation from most gape limited predators, primarily largemouth bass (*Micropterus salmoides*), and have

access to higher energy food sources in the pelagic zones of lakes (Werner & Hall, 1988).

Previous studies have demonstrated the variability of bluegill size among differing

environmental conditions, such as temperature gradients which suggests we will see changes in

bluegill length over time with warming temperatures (Ehlinger, 1990; Ehlinger et al., 1997;

Schneider, 1997; Shoup et al., 2007; Unmuth et al., 1999; White et al., 2020).

Bluegill growth is strongly related to population density and when juvenile population density of

bluegill in a lake reaches a critical point bluegill growth stunts (Chizinski et al., 2010). The

energy in the environment which is bioavailable to juvenile bluegill in littoral zones becomes a

source of intraspecific variation for smaller juvenile year classes. Additionally, instead of

bioavailable energy being allocated towards growth it is shifted to reproduction in stunted

populations with slower juvenile growth that reaches a lowered asymptotic limit – hampering

individuals in the population from reaching large sizes compared to. Research has found that

introducing predators to target bluegill recruitment can be an effective means of restoring larger

sizes to populations. Though bluegill growth is often a factor of population density,

environmental stressors still apply a selective pressure on populations (Ahti et al., 2020; Tomcko

& Pierce, 2001).

In recent decades, increases in climatic and other anthropogenic stressors, such as pollution and

contaminants, noise and light pollution, and biotic invasions whose impacts are known to interact

have been recorded (Reid et al., 2019). I expect that with long term sampling records I will be

able to identify trends in body size across a range of ages of bluegill which can be explained

using ecological habitat data. With this in mind, I seek to answer the following questions: a)

How has the size of bluegill across age ranges, and across the state of Michigan changed over

time?, b)Which environmental factors drive changes in bluegill length the most?, c)What

relationships does length have with the environmental factors?, and d) How do these patterns change across bluegill ontogeny.

Materials and Methods

Datasets

The Institute for Fisheries Research (IFR) houses a collection of cards with historical survey data from Michigan inland lakes as old as 1888. Thanks to a community science effort to transcribe data through the Zooniverse platform (Alofs et al. In Prep), I was able to use this newly available dataset to evaluate historic changes in fish growth.

I used a combination of seven datasets to construct my model of Michigan's changing environment: 1) Historical Inland Lake Summary and Growth Data acts as the scaffolding for the rest of the dataset. The historic lake summary cards hold information on the different surveys, such as the name and location of the lake, sampling date, age groups, minimum, maximum, mean length of each age group, and the number of fish used to calculate the mean. Mean lengths here are reported in inches but converted to millimeters. Records of co-occurring fish species were also used to determine the presence of key bluegill predators including Walleye (*Sander vitreus*), Largemouth Bass (*Micropterus salmoides*), and Northern Pike (*Esox lucius*). 2) The Michigan Department of Natural Resources' Status and Trends (SnT) data complements historic lake summary cards as the modern sampling program in the state (Hayes et al., 2003). The modern sampling program also uniquely identifies each lake within the state's sampling program and is what was used to georeference latitude/longitude, lake depth, and lake area in addition to measures of growth. Further, fish captured for SnT data were collected under a standardized sampling program, using a variety of nets (e. g. Fyke Nets, Gill Nets, Seines) and boom-shocking

equipment. Standard protocols are in place for the volume and intensity of sampling efforts, which is correlated to lake surface area; 3) United States Geologic Survey *Modeled Historical Land Use and Land Cover for the Conterminous United States: 1938-1992* was used to evaluate land-cover across Michigan for the historic period. This raster dataset classifies 14 different land-cover types at a 0.25 km^2 resolution. Land-cover variables were grouped and represented in my dataset as Urban Land Cover, Forested Land Cover, Wetland Land Cover, and Agricultural Land Cover (Sohl et al., 2016); 4) The National Land Cover Database (NCLD) is the contemporary compliment to the USGS historical land cover data. This data set consisted of 16 land-cover types and is a raster which has a 0.0009 km^2 resolution. (Dewitz, 2021); 5) LAGOS-NE is a database of lakes across the northeastern United States, which collects a variety of lake condition factors such as secchi disk depth, alkalinity, and lake-basin footprints. I used lake basin footprints from LAGOS-NE as the area for analyzing land-cover changes. (Soranno et al., 2017) ; 6) US Census data allowed us to track county population for each lake. I used county population, per decade, as a rough proxy of fishing pressure and general anthropogenic activity (Social Explorer, 2022); 7) Degree Day (provided by J. Breck, the Institute for Fisheries Research) summarized the annual number of days where mean surface temperature of the lakes were above 0° C. Degree Days for a given period is calculated as the sum of the daily values of temperature above a specified base value. For example, if the surface water temperatures on three successive days are 14, 16, and 18 C, the Degree Days for that three-day period would be 48 for a base of 0 C, and 33 for a base of 5 C. The Institute for Fisheries Research uses a modification of the method of Shuter et al. (1983) to represent the seasonal temperature regime in a lake by using half a sine wave. With this approach, the Degree Days for the open-water period in the lake can be calculated as the area under the temperature curve that is above a base

of 0 C. The mean surface water temperature during the open-water period can then be calculated

by dividing the total Degree Days by the duration (in days) of the open-water period.

R-8070 4/81

MICHIGAN DEPARTMENT OF NATURAL RESOURCES

Water __School Section Lake__   T. __2S__   R. __14W__   Sec. __16__   FISH GROWTH ANALYSIS

County __Van Buren__   Id. _____   Collection Date __9/27-29/82__

Gear and Methods __Nets & Electro-Stratified Random__

Collected By __Anson__   Section __Fish D-12__   Aged By __Scheppelman__   Section __Fisheries D-12__

Species ↓	Age Group ↺	Number of fish	Length range in inches	Mean length in inches	State avg. length	Growth index (by age group)	Mean growth index for species
Bluegill	0	2	2.0	2.0	2.4		
"	I	13	2.4-3.6	3.0	3.5	-0.5	
"	II	26	3.6-6.0	4.7	4.7	0.0	
"	III	10	5.9-7.0	6.4	5.8	+0.6	
"	IV	6	6.6-8.0	7.4	6.6	+0.8	
"	V	3	7.9-8.4	8.1	7.1	+1.0	+0.2
"	VI	2	8.2-9.1	8.6	7.6		
Largemouth Bass	0	15	2.9-4.4	3.6	4.2	-0.6	
" "	I	24	5.7-8.1	6.6	6.9	-0.3	
.	II	27	7.9-10.4	9.2	9.3	-0.1	
" "	III	14	10.4-12.0	11.3	11.2	+0.1	
" "	IV	3	12.2-12.8	12.4	12.7	-0.3	-0.2
Black Crappie	0	1	2.7	2.7	4.2		
" "	I	3	5.8-6.4	6.0	5.6	-0.4	
" "	II	4	7.1-8.8	8.0	7.2	+0.8	
" "	III	1	8.8	8.8	8.4		
" "	IV	7	10.0-10.6	10.3	9.2	+1.1	+1.1

Several species may be listed on one sheet

Figure 1. Example of growth card, digitization makes hardcopy data available to conduct computer analysis.

All together the combined dataset represents 11,109 unique observations of mean bluegill length

at age. 3,368 of which come from SnT data, and the remaining from historical growth cards.

Recorded bluegill ages span from zero (young-of-year) to 18. These data span across both

peninsulas, from 1888 – 2019, however growth data were only available for two lakes before

1950, therefore, to reduce the possible influence of outliers, I only use data from 1950 and later

totaling 1069 inland lakes within the state of Michigan. Ages zero and 11-18 all have less than

100 observations and so were not included in the model. Ages one to eight all had more than 500

observations, so I restrict my models to only these age groups.
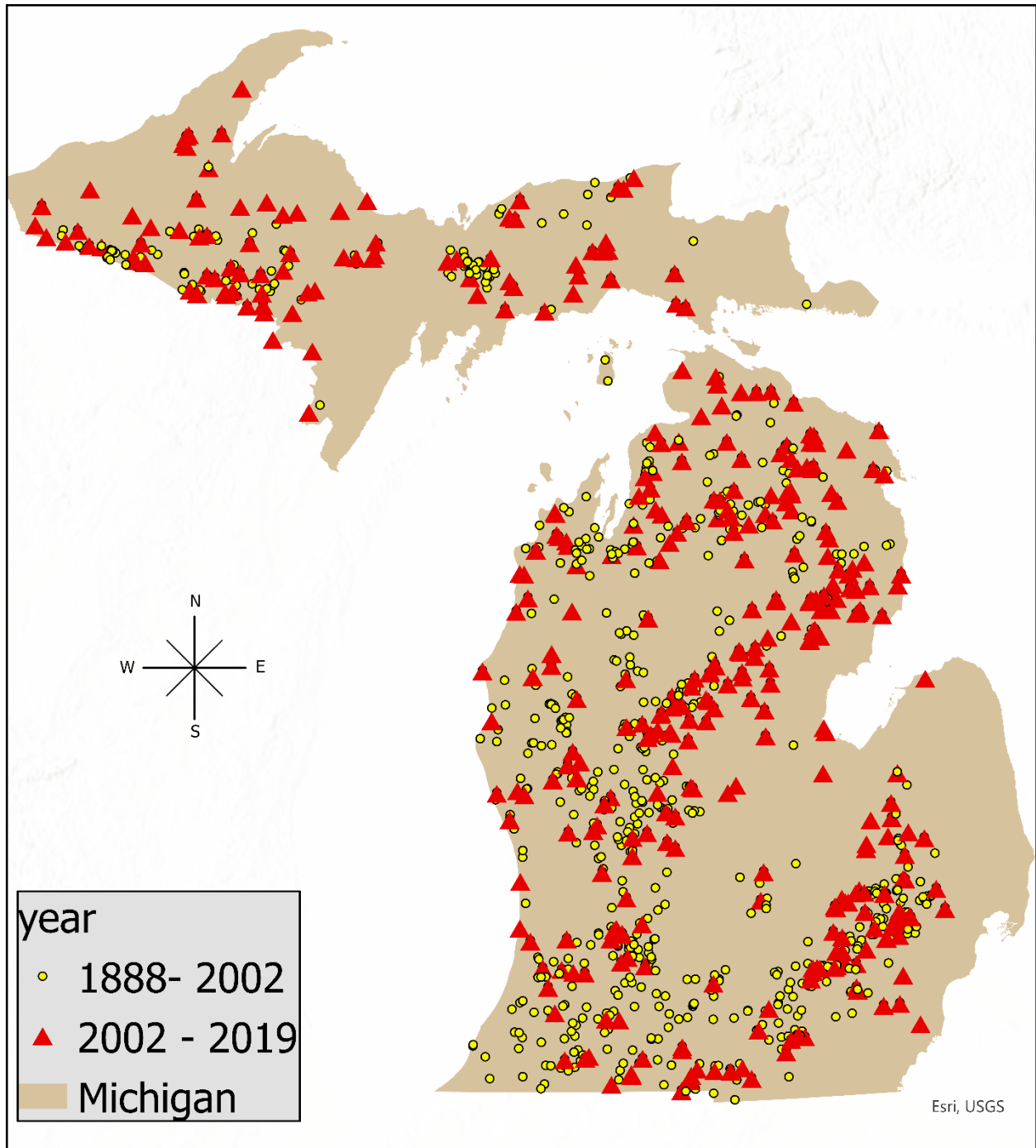
Figure 2 Map of study area. Circles indicate a lake sampled before the contemporary Status and Trends monitoring system - which are indicated by triangles.

I used Geographic Information System (GIS) ArcGIS Pro to quantify land-use land-cover data

from both the USGS (Sohl et al., 2016) and NLCD (Dewitz, 2021). I used lake-basin footprint

shapefiles from the LAGOS-NE dataset to set bounds on the influence of the land and to

spatially link the growth data (Soranno et al., 2017).

Table 1. Statistical summary of the continuous variables analyzed.

	Min	Max	Mean	Standard Deviation	Sample Size
Mean Length (mm)	27.94	304.8	151.17	48.52	
Age 1	27.94	215.9	71.13		849
Age 2	43.18	223.52	103.34		1528
Age 3	68.58	254	130.63		1956
Age 4	91.44	248.92	153.95		1933
Age 5	96.52	248.92	171.29		1664
Age 6	121.9	264.2	186.3		1261
Age 7	127	304.8	186.3		867
Age 8	142.2	276.9	210.2		510
Year	1955	2019	1988	16.27	
Month	1	12.000	31709.50	24.81	
% Forest	0%	100%	45%	26%	
% Wetlands	0%	100%	14%	13%	
% Urban	0	97%	8%	14%	
% Agricultural	0	93%	27%	26%	
Lake Area (Ac)	2.44	5092.69	295.51	433.49	
Mean Lake Depth (ft)	0.500	141	13.78	9.00	
County Population	3447	2337891	158088.73	298578.57	
Degree Days	2749.19	6522.38	4746.75	1640.47	

Statistical Analyses

All statistical analyses were conducted in R (R Core Team, 2021). I used simple linear

regressions to model the change in mean length over years for each age class, with an α of 0.05

to determine significance. Summary statistics including minimum and maximum value, mean and standard deviation can be found in table 1.

Given the heterogenous format of this dataset, I used Boosted Regression Tree (BRT) modelling to evaluate the relative influence of individual variables on mean body size at age(Chu et al., 2016; Elith et al., 2008). In contrast to linear models, BRT models are robust in their ability to oversee datasets with multiple data formats such as different distributions or non-nominal data. BRT models can also account for missing values or NAs in the dataset which is an advantage when dealing with "patchy" data availability such as in this project. For ages 1 to 8, I use BRT models to evaluate the relative influence of predictor variables on mean body size, and to examine the impact these predictors have while also accounting for the impact of other predictors.

BRT finds relationships in data through the machine learning process called boosting, which combines many different regression trees to improve predictive performance (Elith et al., 2008). The regression trees compare predictor variables to a given response (such as mean length at age) and make groupings which link the most homogenous spaces of the response. Many large trees are constructed using this method, combined through boosting, and cross-validated with a subset of the data. BRT models quantify the relative influence of the predictor variables on the response based on the number of times that a given predictor was found to be important in evaluating a response. Thousands of trees are often constructed, the number determined through manually set learning rates, interaction complexity, and stochasticity or bag rate (Elith et al., 2008). For my models, a learning rate of 0.001 was used, modelling fifth degree interactions, and a bag rate of 0.5. Modelling was accomplished with the "dismo" and "gbm" packages (Greenwell et al., 2020; Hijmans et. al, 2021) in R. The distribution of some variables (county

population, lake area, and mean lake depth) made interpretation difficult due to high counts of observations occurring across a limited value range. To increase interpretability, I used a log-e transformation to distribute observations more evenly. For my complete model, I used the mean length observations of each age class as a dependent predictor, while the explanatory variables which the boosted regression model were fitted to are the year and month the survey occurred; proportion of land cover which was urban, wetland, forested, or agricultural; presence indicators for walleye, largemouth bass, northern pike, and yellow perch; degree days; mean lake depth and surface area; and the population of the surrounding county as reported by the closest US Census. Mean lake depth, lake surface area, and county population are all transformed with a natural log transformation. I ran two additional models, one with only degree days as an explanatory predictor and another with degree days, log-e transformed mean lake depth, and log-e transformed lake surface area. The additional models aided in determining the impact of climate compared to other values on model performance. Multivariate models were simplified to remove variables which were redundant in model creation by removing variables one at a time until the deviance explained by the model failed to explain more than the mean deviance.

I evaluated the accuracy of these models using pseudo-R-squared values (Chu et al., 2016). Pseudo-R-squared quantifies the reduction in predictive deviance as the number of trees are increased. This statistic is calculated as, 1- (Residual Deviance/ Total Deviance). Like an R-squared value, it is a ratio which approaches 1 as predictive performance increases.

The results of these models were also interpreted using partial dependence plots, which show the effect of predictor variables on size at age – independent of the influence of other predictors. I display only the predictors which explain the top eight relative influences for simplicity.

Results |

I found changes in mean length varied by age group (Figure 3). Age classes one to four have a negative relationship between mean length and year, and beyond age class five the relationship becomes positive. The changes in body size over time are significant trends in most year classes; p-values for age groups were less than 0.001, except for ages five and eight which were 0.093, and 0.052, respectively. R^2 values for these linear models ranged from less than 0.001 to 0.28 and explain a small amount of the variation seen in growth. In general, juvenile bluegill ages four and younger are reaching smaller sizes at these ages, whereas mature bluegill age five and older are not experiencing changes in their body size or are reaching larger sizes.
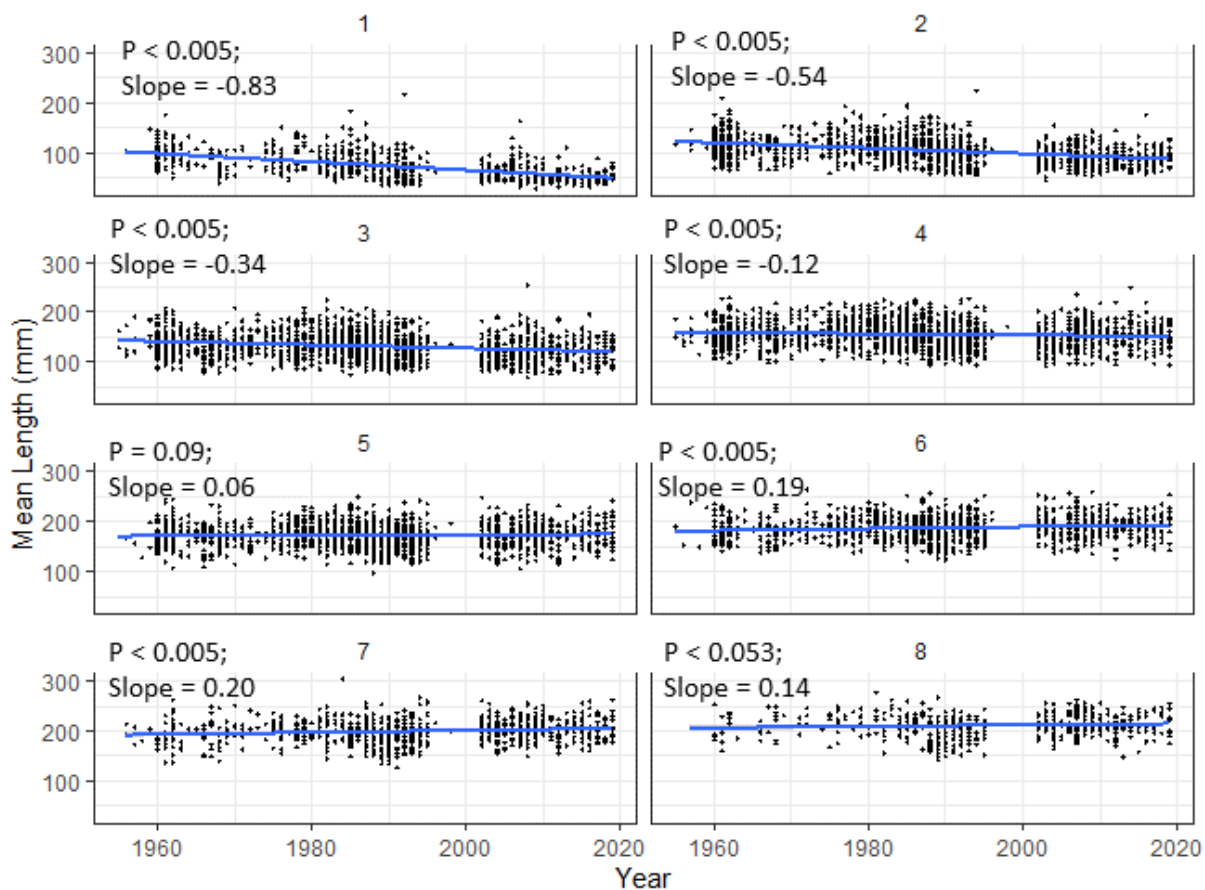
Figure 3. Changes in mean length over time. Regression line takes the form $Length = m * Year + b$, where m is the slope of the regression line. R^2 values, ascending by year, are as follows: 0.29, 0.13, 0.04, 0.005, 0.001, 0.01, 0.02, and 0.01.

Influence of Environmental Factors

The percentage of deviance explained by BRT models increases with factors added to the model, regression trees using only Degree Days as an explanatory factor pseudo-R-squared values range from 0.031 to 0.27 and was higher for ages seven and eight than for other models. Adding lake morphological factors, mean depth and surface area, improves explanatory power to 0.07 to 0.33. Finally, adding all collected environmental factors model performance ranged from 0.22 to 0.61 (Figure 4).
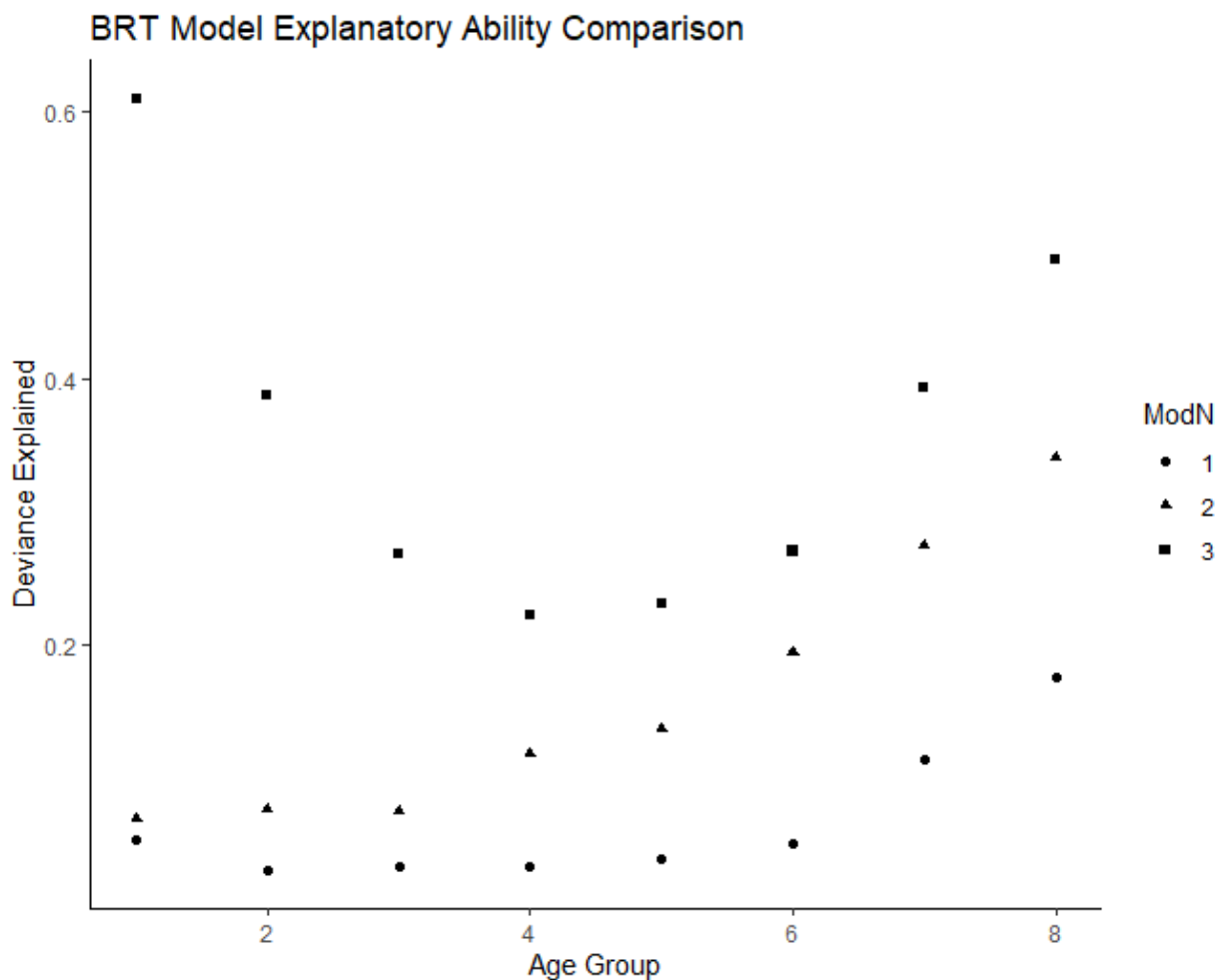

Figure 4: Pseudo R-squared values for three models (shown as ModN, or Model Number) with 1,3, and all environmental factors included.

Pseudo-R2 values are highest in the final model for ages one and eight, explaining a range of deviance from 22% to 61%. The relative influence of the environmental factors varied by age class as well; of the eight age classes modeled, mean depth was the most influential factor in ages four, five, and six (Table 2). Age classes one, two and three were both influenced the most by the month in which the survey was conducted; the final two age classes seven and eight are most influenced by the population of the encompassing county. Degree days tend to be the third or fourth most influential factor across age groups, though its influence increased in older age classes. Finally, land-use land-cover factors show a marginal increase in influence with bluegill age – only being the third most influential factor for ages seven and eight. In juvenile age classes, land-use land-cover factors are the least influential, and agricultural land-use land-cover tended to be the most influential of the different cover types.

Table 2: Influence Rank 1-8 for each age group, with relative influence in parentheses. Bolded factors have been log transformed. Blue cells indicate lake geomorphic features, yellow cells indicate Degree Days, and green cells indicate land-cover variables.

Influence Rank	Age 1	Age 2	Age 3	Age 4
1	Month (47.19)	Month (46.46)	Month (28.20)	**Mean Depth (22.74)**
2	Year (15.44)	Year (14.64)	Degree Days (12.51)	**County Population (15.51)**
3	**County Population (9.14)**	Degree Days (12.49)	**Lake Area (11.45)**	Degree Days (15.01)
4	Forests (5.43)	**Mean Depth (11.25)**	Year (9.19)	Month (13.97)
5	Degree Days (5.17)	**Lake Area (10.53)**	**Mean Depth (10.02)**	**Lake Area (13.33)**
6	Urban (4.62)		Agriculture (6.59)	Agriculture (11.95)
7	**Mean Depth (3.69)**		**County Population (6.46)**	Year (7.46)
8	Agriculture (3.52)			

Influence Rank	Age 5	Age 6	Age 7	Age 8
1	**Mean Depth (22.23)**	**Mean Depth (24.49)**	County Population (25.76)	**County Population (23.13)**
2	**County Population (15.18)**	County Population (24.44)	Mean Depth (24.41)	Degree Days (15.41)
3	Degree Days (13.63)	Degree Days (15.22)	Degree Days (15.35)	**Mean Depth (15.40)**
4	Agriculture (12.63)	**Lake Area (13.92)**	Agriculture (13.13)	Agriculture (11.92)
5	**Lake Area (10.13)**	Year (11.04)	Year (11.65)	Wetlands (9.68)
6	Wetlands (7.42)	Agriculture (10.87)	**Lake Area (9.68)**	**Lake Area (6.79)**
7	Forests (6.66)			Urban (5.19)
8	Year (6.63)			Forests (4.45)

Partial Dependence Plots – How do factors impact growth?

Adding predictors to BRTs of size at each age clarified the impact of individual factors by smoothing relationships in partial dependence plots while the underlying patterns remained similar regardless the number of predictors in the model. Each predictor's relative influence varied across age groups, but the patterns of variable effects stayed relatively consistent across age groups and variable combinations. Lake geomorphological factors and land-use land-cover factors showed a change in effect, where the growth response from bluegill was age dependent, juveniles showed decreases in size at age whereas adults experienced increases in size (Fig. 5). Forested land-cover and urban land-cover both had a negative effect on juvenile growth, which was positive once bluegill reached age five. While increasing wetland and agricultural land-covers had a negative effect on mature bluegill growth, and a positive effect on juveniles. Lake geomorphological factors, such as mean lake depth (Fig. 5) and lake area, had a negative effect on juvenile growth. In mature age classes, this was a positive effect.

County population had a negative effect on the mean length of all age groups, an effect which was more pronounced in mature age classes, or at the largest counties in juvenile ages (Fig. 6). Degree days also had an overall negative relationship with mean length, with length declining significantly past 4000 degree days across years (Fig. 7). The month each sample was collected maintains a logistic growth relationship, with a noticeable increase in growth occuring in the late summer. The largest increase in size between spring and fall occured in juvenile age classes (Fig. 8).
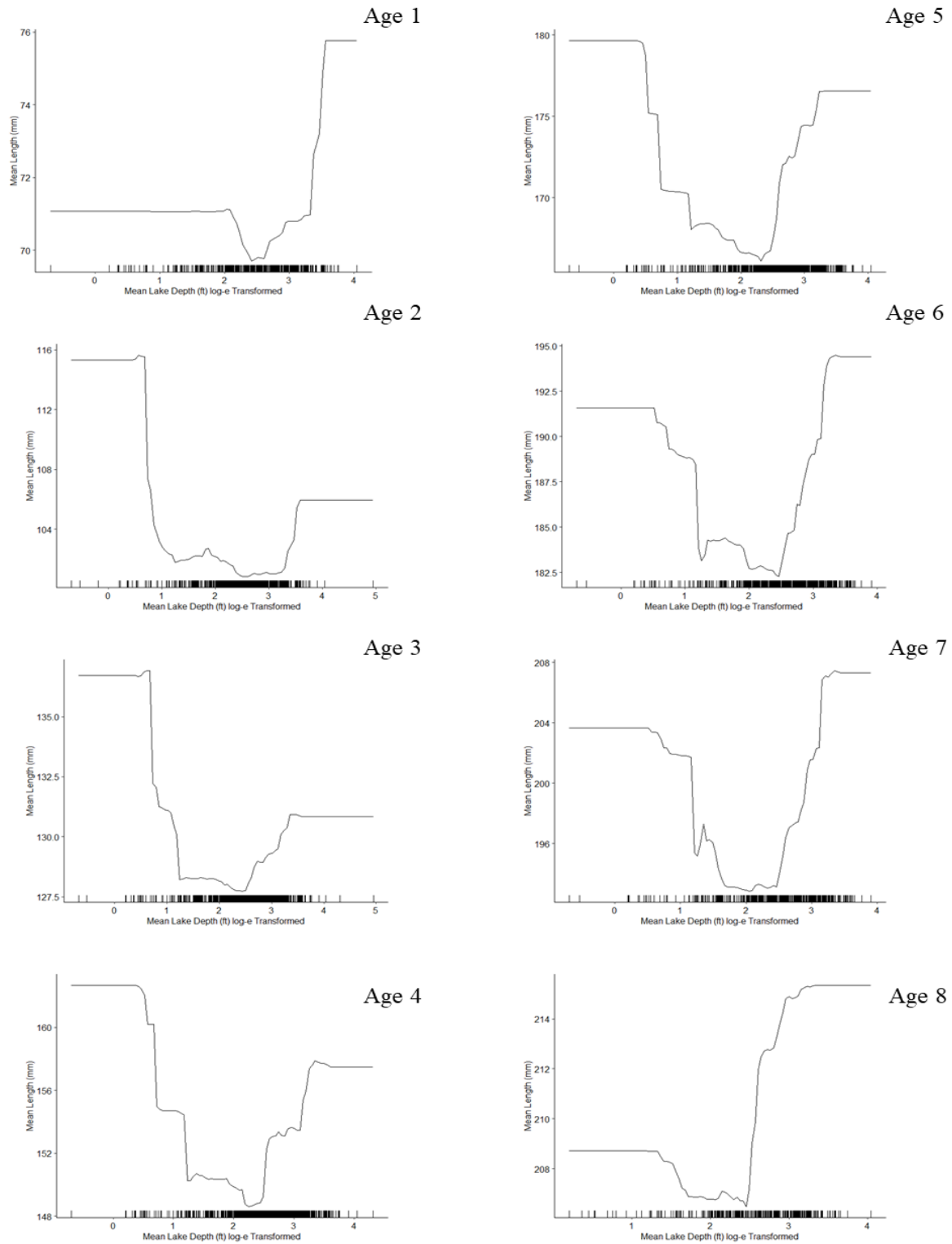
Figure 5. Partial dependence plots showing the effect of mean depth on bluegill mean length.
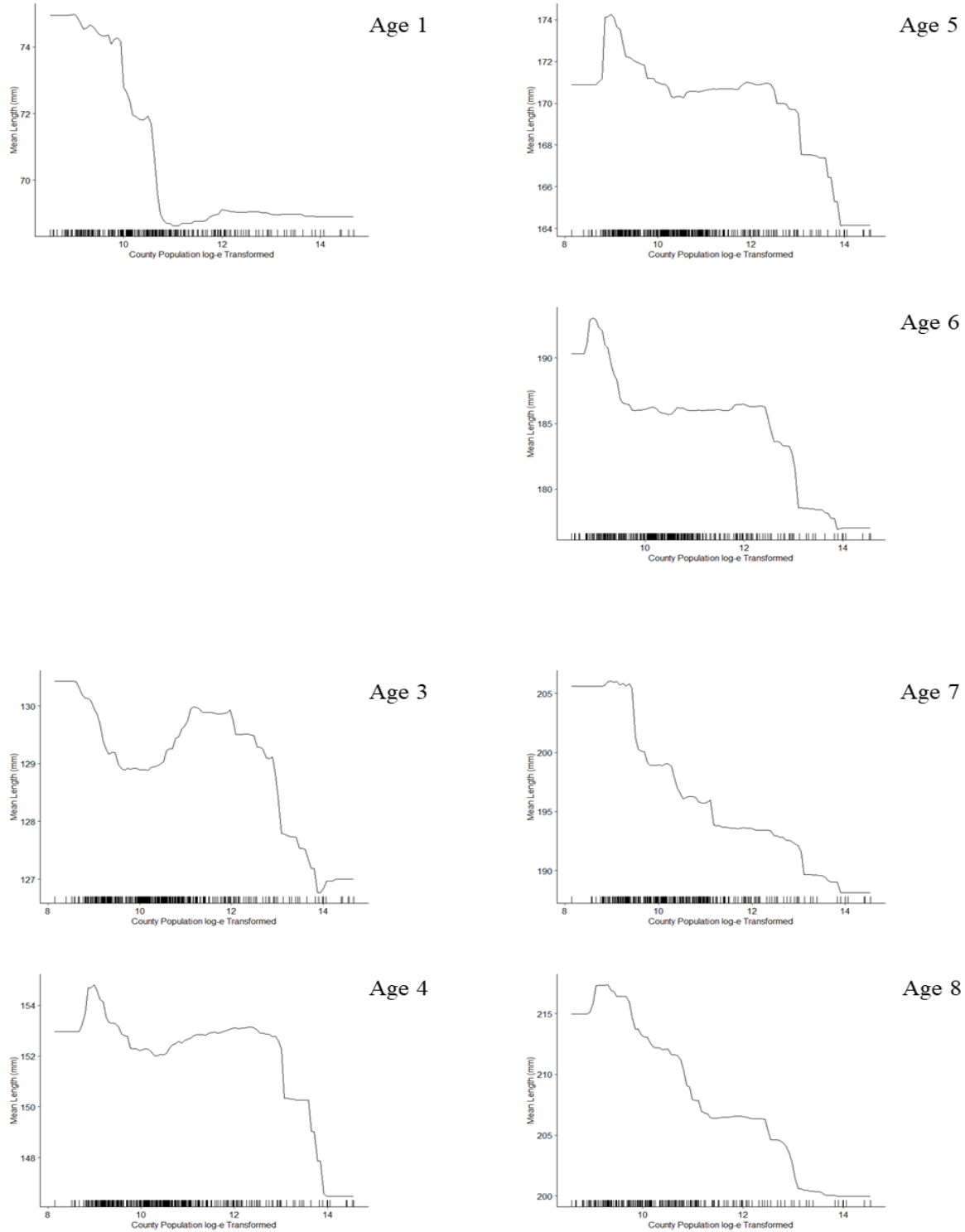
Figure 6. Partial dependence plots showing the effect of the surrounding county population, log-e transformed, on the mean length for age groups one to eight. In my BRT models, county population was removed in simplifying the predictor set for age 2.
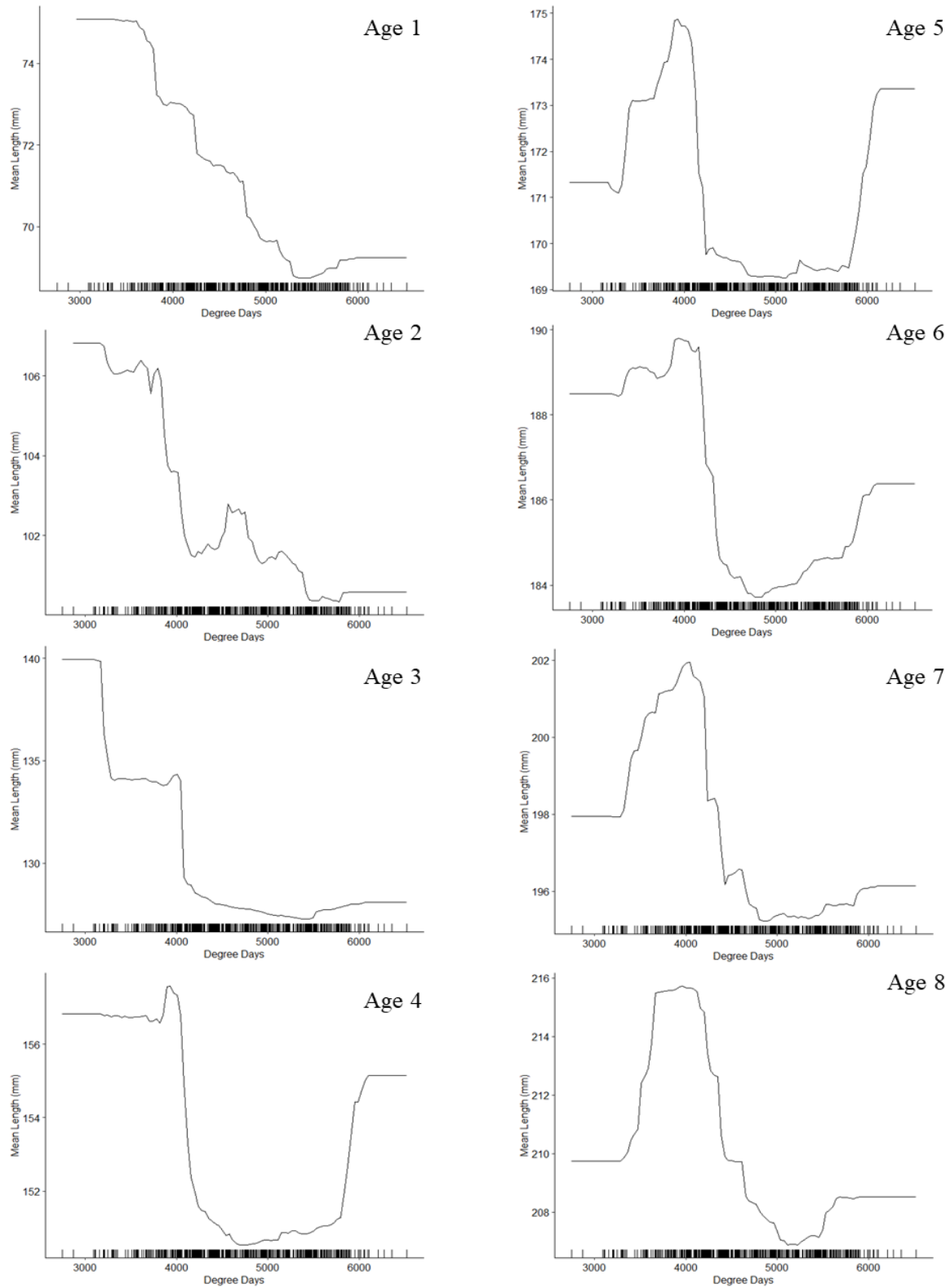
Figure 7. Partial Dependence Plots representing the effect of Degree Days on mean length. These plotted relationships demonstrate the effect on mean length, while taking the mean effect of the other variables into account.
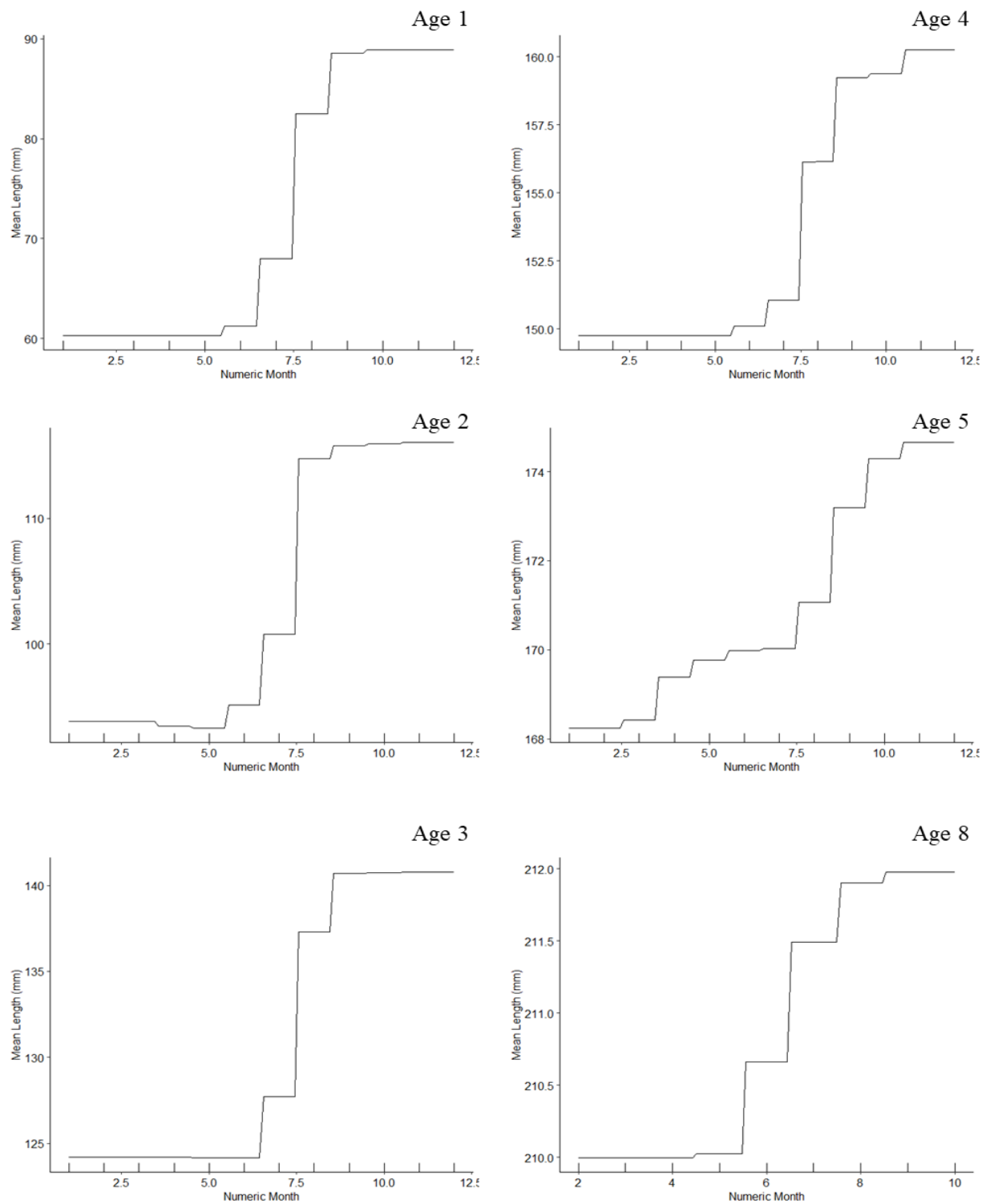
Figure 8. Partial dependence plot showing the effect of sampling month on bluegill size at age. While the shape of plots is similar, note the change in y-axis scale which becomes smaller with age.

Discussion |

Over the 69-year time span of this study, juvenile bluegill have been growing slower and some mature age classes of bluegill have been growing faster. Results from my linear regression models indicate the shift in growth trend happens after age five, which has not significantly experienced any changes in growth. The most influential factor related to bluegill growth for ages one to three, and second most influential for age four, was the month in which the survey was conducted, with most of the growth occurring over the summer months from June to September, overlapping with the spawning season for bluegill. As fishes age, the rate of growth declines and, as expected, growth achieved over the summer decreases with age group (Patnaik et al., 1994). Wagner et al. (2007) also reported seasonality (Fall, Winter, Spring, Summer) to be the most important factors in models of bluegill growth for ages two and three, though they are treated as dummy or control variables. The impact of sampling month may be related to temperature variations within a given year, a potential confounding variable for which my data currently does not have the resolution to account.

As bluegill age, mean lake depth (for ages five and six) and the population of the surrounding county (ages seven and eight) have stronger relative influence on growth. Mean lake depth informs how much littoral habitat there is in each lake, as lakes increase in mean depth generally the proportion of shallow, littoral zones decrease. Bluegill rely on littoral zones for breeding and refuge from predators, both mechanisms of recruitment for the species. As bluegill become large enough to avoid predation, they also become less adapted for these zones as they change morphologically, adapting to conditions of the open water (Bell & Jacquemin, 2017). For older and larger bluegill then, the amount of deep, open water space available to be inhabited becomes an increasingly important habitat factor. In my model county population was used to

approximate fishing pressure in the absence of mortality data. The relationship between county population and size is negative across all age classes but increases is increasingly influential for older age classes. Recreational fishing is highly size selective, removing the largest and often oldest individuals from a population, lowering the mean length for older bluegill living in highly populated counties (Rypel, 2014).

As ectothermic organisms, fish metabolic activity is regulated by environmental temperatures and given all else is equal with an increase in Degree Days, the number of days available for growth, – we expect that growth should increase (Brown et al., 2004). Additionally, we expected that temperature would be highly influential in determining growth. However, degree days were not as influential as the above-mentioned factors, typically being second or third most influential. Partial dependence plots from my models show that as the average number of degree days experienced goes up, growth increases briefly in some cases (particularly ages five, seven, and eight) before sharply declining. There are several explanations for declines in size with increasing degree days including temperatures exceeding the optimum for growth (Have & Jong, 1996), lack of productivity and food resources to meet increasing metabolic demands (Sheridan & Bickford, 2011), density-dependence or other ecological interactions.

Bluegill growth has been strongly linked with density dependent mechanisms, where larger populations of bluegill grow more slowly. In stocked ponds the growth of bluegill populations shows an inverse relationship with density (Krumholz, 1949; Latta & Merna, 1976). Conversely, juvenile mortality can correspond to faster growth of juvenile year classes (Partridge & DeVries, 1999). Management efforts to increase bluegill size, and reduce stunting, often leverage mechanisms that target juvenile survivorship such as increasing predator densities through stocking, or via fish kills (Neal, 2017; Schneider & Lockwood, 1997). Other warmwater adapted

centrarchids, such as largemouth bass have demonstrated increased fecundity and recruitment given an increase in degree day values (Casselman, 2002). It is likely then that decreases in bluegill growth with increasing degree days may similarly be due to increased fecundity and higher density juvenile populations. High density populations of bluegill consume many of the resources in their environment and are unable to leverage enough energy to grow to large sizes (Mittelbach, 1983). Natural reductions of density via mortality (e. g. predation, overwinter starvation, disease) for juveniles however are often mediated by other environmental factors, such as water temperature, spawning/hatching time (subsequently the length of first growing season), nutrient input, and productivity/food abundance (Casselman, 2002; Latta & Merna, 1976). My model captures the variation of many environmental factors that mediate these processes and are indirectly represented through changes in bluegill growth.

My model performance matches or improves upon other attempts to model bluegill growth with environmental factors. Studies such as Tomcko and Pierce, (2001) similarly use variables such as temperature, depth, and lake area to analyze relationships between bluegill growth and environmental factors. Their analysis, however, also included lake alkalinity, shoreline development and secchi-depth, explaining 16-33% of variation in bluegill size. Later, in 2005, the same authors improved their models by focusing on population density factors, such as year class strength, to explain 19-51% of variation in size at age, similar to models presented here (Tomcko & Pierce, 2005). With pseudo-R^2 values ranging from 0.22-0.61, my model is effective at predicting mean lengths for the different age classes and improves on the explaining variation in growth compared to other models focusing similarly on landscape factors.

Despite best practices, my dataset exhibits shortcomings. Historical records do not include estimates of population sizes for the different age classes, limiting our ability to conduct an

analysis with a direct measure of density. Future analyses could include bluegill CPUE to compensate for the lack of density measures. Similarly, the density of predators and competitors could be useful factors to consider for juvenile age groups. Other studies, such as Tomcko and Pierce (2001), also suggest that environmental variables such as secchi depth that could improve model performance.

I am also missing data from a small period in-between the different sampling programs from 1996-2002. Missing data exists in other storage formats that were outside the accessibility of this study but may be applicable for future research. Additionally, sampling methods have changed over the period of my study and particularly between the two survey datasets. Standardization of sampling methods across the state has led to better catches of juvenile age classes in SnT data. The standardization of bluegill sampling methods might suggest that historical data was biased to larger sizes, a possible explanation of decreasing lengths in juveniles, however using the mean length as a measure of body size should mitigate against that bias.

Future studies should look to investigate other historical data formats. Museum specimens can be a reliable source of information describing geometric morphometric changes in bluegill, which are capable of characterizing changes experienced by bluegill more thoroughly than mean length alone can. Large scale temporal shifts in body shape may be accompanying the shifts in size reported in the study here, which could reveal an explanatory relationship. With more complete population information on species assemblages in these lakes or by including relative abundance of bluegill to account for intraspecific population dynamics more accurately, I may be able to account for variation more accurately in growth. Further, this work could be expanded upon by investigating the applicability of these models to other inland lake fish species.

Conclusions |

In this study I used long term datasets to parse out the impacts of the changing environmental variables on fish growth by examining average size at age of bluegill in Michigan from 1950-2019. This approach to analysis was able to explain 22% to 61% of the deviance in the mean length at an age class for bluegill, improving on previous models. Over the 69 years of my study data, length at age of juvenile bluegill ages one to four declined, and length at age of mature ages six and older increased. I found the influence of environmental factors to be variable across age groups, though the effects they have on the mean length of those age groups are functionally similar, indicating that for some predictors ontogenetic variation is less important for structuring bluegill size. Literature suggests that the impact of changing environmental variables is overlapping and could be obscuring the true nature of the relationships between the average size of a bluegill at a given age and the recent changes in climate. In my models degree days had an unexpected negative relationship with bluegill growth, potentially due to intraspecific competition of juveniles. Further investigation is needed to clarify these relationships specifically.

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