Factors Affecting Largemouth Bass Size Structure at Wheeler and Guntersville Reservoirs, Alabama

by

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A thesis submitted to the Graduate Faculty of
Auburn University
in partial fulfillment of the
requirements for the Degree of
Master of Science

Auburn, Alabama
August 1, 2015

Keywords: reservoir management, Largemouth Bass,
population modelling, natural mortality

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Abstract

Understanding the characteristics of a fish population is vital to the assessment and management of the stock. Size structure and abundance are two such characteristics of a population and they have the potential to vary spatially and temporally. Causes for this variation between and within stocks are not well understood. Comparing largemouth bass (*Micropterus salmoides*) growth, mortality, and year-class strength in Wheeler and Guntersville reservoirs, two Alabama impoundments with observed size structure differences, provides an opportunity to investigate factors that affect population size structure. The study was executed by 1) evaluating between-lake differences in size structure, growth, maturity, condition, and diet, 2) quantifying associations between natural mortality and early-growth rates within and between the two populations using a catch curve analysis, 3) evaluating the sensitivity of between-lake differences in relative abundance of 500-mm and larger largemouth bass to changes in growth parameters, natural mortality, fishing mortality and fishing regulations within the estimated parameter ranges for these lakes using a per-recruit age structure model, and 4) fitting a statistical catch-at-age analysis (SCAA) to reconstruct year-class strength and fishing mortality time series' using age composition and relative abundance data from spring electrofishing surveys.

Results of the between-lake comparison suggests that Wheeler largemouth bass grew faster, which may have constrained the population to a higher mortality and shorter life expectancy, and thus a lower proportion of large fish. The catch curve analysis demonstrated that differences in early growth could explain the variation in natural mortality of largemouth bass and the sensitivity analysis of the relative abundance of 500 mm largemouth bass between lakes suggested that natural mortality likely influences size structure more than growth alone. Results of the SCAA indicated that recent year-class strength estimates were robust to changes in model assumptions and correlations among lake were weak. The data suggest that variation in early growth could be attributed to differences in diet, possibly due to habitat availability differences; however, this was not confirmed with bioenergetics modelling. This study reiterates the interrelated nature of life history traits growth, mortality and age-at-maturity where reproductive fitness is optimized by adjusting age-at-maturity given a trade-off between growth and mortality.

Acknowledgments

I would first like to thank my advisor Dr. Matthew Catalano for giving me the opportunity to purse a graduate degree in fisheries and for his guidance and support throughout my studies at Auburn University. I would also like to thank committee members Dr. Dennis DeVries and Dr. Russell Wright who provided valuable input and guidance through my entire graduate program. A special thanks goes to Tammy DeVries as well as the many graduate students and technicians who helped with extensive lab and field work: Jeff Buckingham, John Fennell, Gary Grove, Sean Lusk, Braxton Setzer, Adrian Stanfill, and Ben Staton. I thank Alabama Department of Conservation and Natural Resource for interest and funding this project. Finally, I thank my family for always supporting my decision to pursue my passion for fisheries.

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I. Introduction

Understanding the characteristics of a fish population is vital to the assessment and management of the stock. Size structure and abundance are two such characteristics of a population and they have the potential to vary spatially and temporally. Causes for this variation between and within stocks are not well understood. Differences in individual fish growth and mortality are likely influences on size structure and abundance. This understanding is important because changes in size structure of a fish stock can have implications for ecological processes such as recruitment via stock-recruitment relationships (Ricker 1954; Beverton-Holt 1957) and the composition and abundance of other species due to complex interactions via trophic cascade (Kitchell and Carpenter 1993). Variation in size structure and abundance can also dictate variation in catch rates and composition of commercial and recreational fisheries. If changes in growth or mortality can result in changes in size structure and abundance, it is vital to investigate the mechanisms for this process.

Growth has been positively correlated with size structure both spatially (Novinger and Legler 1978; Miranda 1983) and temporally (Carline et. al 1984) and mortality has been inversely correlated with size structure (Novinger and Legler 1978; Miranda 1983; Beamesberfer and North 1995). Modelling by Carline et al. (1984) showed a negative linear correlation between size structure and mortality. Variation in recruitment over time can also influence size structure. Observed changes in size structure of a bluegill (*Lepomis marcochirus*) population in Ross Lake, Ohio were attributed to the recruitment variation, rather than changes in age-specific mortality or growth (Carline et al. 1984). Including recruitment variation in a population model has been shown to cause fluctuations in size structure (Carline et al 1984; Gabelhouse 1984) and Carline et al (1984) concluded that, in medium to large impoundments, recruitment was likely to have more influence on size structure than either growth or mortality.

Largemouth bass (*Micropterus salmoides*) stocks in Alabama provide an opportunity to investigate how growth, mortality, and recruitment affect size structure and how these factors relate to one another. Largemouth bass is an important recreational sport fish in Alabama and statewide declines in catch rates of fish greater than 500 mm in the late 1990s and early 2000s due to outbreaks of largemouth bass virus (LMBV; Maceina and Grizzle 2006) raised questions regarding factors influencing the size structure of largemouth bass stocks in these reservoirs. Two popular largemouth bass fisheries, Tennessee River impoundments Lake Guntersville and Wheeler Reservoir, followed the statewide declines. Since the declines, statewide and Lake Guntersville catch rates have returned to historical norms, while Wheeler Reservoir average catch rates are in the bottom 40% of Alabama Reservoirs since the 1997 LMBV outbreak (Abernethy 2012). Variation in growth, mortality, and recruitment within and between lakes may explain the differences in size structure between Lake Guntersville and Wheeler Reservoir.

My thesis research investigates whether recent differences in growth, mortality, and recruitment between Lake Guntersville and Wheeler Reservoir can explain the variation in size structure between lakes. In Chapter II, I compare the current state of largemouth bass populations at Guntersville and Wheeler reservoirs to explain variation in size structure by 1) evaluating between-lake differences in size structure, growth, length and age-at-maturity, condition, consumption, and diet composition, 2) quantifying associations between natural mortality and early-growth rates within and between the two populations using catch curve analysis, and 3) evaluating the sensitivity of between-lake differences in relative abundance of 500-mm and larger largemouth bass to changes in growth parameters, natural mortality, fishing mortality and fishing regulations within the estimated parameter ranges for these lakes using a per-recruit age structure model. In Chapter III, I compare recent recruitment and fishing mortality trends to explain variation in current size structure between lakes by 1) fitting a statistical catch at age analysis (SCAA) model to reconstruct recruitment and fishing mortality time series' using age composition and relative abundance data from three Alabama reservoirs (Demopolis Reservoir, Lake Guntersville, and Wheeler Reservoir) of varying sampling frequencies to evaluate model sensitivity to missing data, 2) conducting a sensitivity analysis of the SCAA under a variety of scenarios that differ in supplemental data inputs, assumed natural mortality, fishing variability, and relative data weighting parameters, and 3) correlating recruitment time series' between reservoirs to assess differences in recent trends. These two approaches allowed me to evaluate if there are differences in growth, mortality and recruitment between lakes, and which of these differences likely contributes the most to the current variation in size structure.

II. Factors affecting largemouth bass size structure at Guntersville and Wheeler Reservoirs, Alabama.

Abstract

Understanding the characteristics of a fish population such as size structure and abundance is vital to the assessment and management of the stock. These characteristics of a population have the potential to vary spatially and temporally and causes for this variation between and within stocks are not well understood. Management of largemouth bass stocks could benefit from a better understanding of the mechanisms influencing size structure. This study investigated factors affecting size structure of largemouth bass populations at Guntersville and Wheeler reservoirs, Alabama. The goals of this study were to 1) evaluate between-lake differences in size structure, growth, maturity, condition, and diet, 2) quantify associations between natural mortality and early-growth rates within and between the two populations using a novel catch curve analysis, and 3) evaluate the sensitivity of between-lake differences in relative abundance of 500-mm and larger largemouth bass to changes in growth and mortality. Results of the between-lake comparison indicated that Wheeler Reservoir largemouth bass exhibit faster early growth, higher mortality and shorter life expectancy, and thus has a lower proportion of large fish relative to Lake Guntersville. The catch curve analysis demonstrated that variation in mortality between lakes were consistent with an early growth-natural mortality associations rather than a lake specific effect. A per-recruit simulation model indicated that natural mortality rates likely influence size structure more than growth alone in these lakes. However, natural mortality differences alone did not fully explain between-lake differences in size structure. Thus, growth-mortality trade-offs may explain some of the variation in size structure, but other factors such as recent recruitment variation may also be important.

Introduction

The size structure of a fish population has important ecological and management implications. Size structure refers to the length distribution of a stock and is important because changes in size structure can have implications for ecological processes such as recruitment via spawning stock-recruitment relationship (Ricker 1954; Beverton-Holt 1957) and the composition and abundance of other species due to complex interactions such as trophic cascades (Kitchell and Carpenter 1993). It may influence recruitment dynamics via effects on reproductive investment by adults (Jennings et al. 1997, Cardinale and Arrhenius 2000), and may also influence the fish community via shifts in size-selective predation (Boxrucker 1987; Walters and Post 2008; Shackell et al. 2010). Preserving large size structure is important for maintaining long-term fishery sustainability in marine stocks because of the positive influence of parental fish size on fecundity and larval survival (Berkeley et al. 2004).

Fish population size structure varies spatially among stocks and temporally within stocks and causes for this variation need further evaluation. Size structure distributions result from the counteracting effects of growth, mortality, and recruitment on the relative abundance of large and small individuals. Thus, changes in growth or mortality can result in changes in size structure (Miranda 1983; Carline et. al 1984; Beamesberfer and North 1995). Understanding the sensitivity of size structure to changes in growth and mortality could improve predictability of population dynamics across stocks and over time.

Fish growth has a strong influence on size structure over time (Carline et. al 1984) and space (Novinger and Legler 1978; Miranda 1983), and age structured population simulations have confirmed a positive influence of growth on the proportion of large individuals within a population (Anderson and Weithman 1978; Carline et al. 1984; Modde and Scalet 1985). Growth is in turn affected by physical, ecological, and physiological processes. Physical habitat structure, such as macrophyte density, can influence growth (McCauley and Kilgour 1990; Bettoli et al. 1992; Wrenn et al. 1996; Brown and Maceina 2002) and variation in diet composition or consumption rate brought on by differences in habitat or forage availability can also influence growth (Shelton et al. 1979; Timmons et al. 1980; Keast and Eadie 1985; Bettoli et al. 1992). Furthermore, changes in maturity schedule can cause variation in growth because growth slows when energy is allocated toward gonad development and spawning activities (Mangel and Stamps 2001).

Size structure has also been empirically related to mortality rates (Novinger and Legler 1978; Miranda 1983; Beamesberfer and North 1995). Higher mortality rates can result in size distributions shifted toward smaller individuals because fish do not live long enough to reach large sizes. Carline et al. (1984) showed a negative linear relationship between the proportion of large individuals within a population and mortality. Changes in natural mortality caused by increases presence of disease (Maceina and Gizzle 2006), or changes in fishing mortality such as changes in exploitation rate or size-selective harvest (Wilde 1997; Allen et al. 2008) can influence total mortality.

However, growth and mortality are not independent. Growth, mortality, and age-at-maturity are typically interrelated among and within stocks. Attempts have been made to quantify relationships among growth, mortality, and other variables to predict natural mortality rates (Pauly 1980; Hoenig 1983; Myers and Doyle 1983; Jenson 1996). Pauly (1980) estimated a relationship between instantaneous natural mortality (M) rate and $L\infty$ (maximum asymptotic length), K (1/year, growth rate), and T (^{0}C, mean annual water temperature). Jenson (1996) used life history theory to suggest that $M = 1.5\ K$ while Hoenig (1983) estimated a relationship between M and maximum age. This trade-off between growth and mortality is a response to optimizing reproductive fitness in different environments (Winemiller and Rose 1992). Reproductive fitness is further optimized by adjusting age-at-maturity given this trade-off between growth and mortality (Mangel and Stamps 2001). Within the constraints of life history strategy there is a continuum of intraspecific plasticity in growth, mortality, and age-at-maturity parameters (Carline et al. 1984; Beamesderfer and North 1995; Shuter et al. 1998; Allen et al. 2008). Shifts in these parameters, in an effort to optimize fitness, can have implications for size structure. A fish stock with fast growing, early maturing individuals with high mortality and short life expectancy is prone to having few large individuals and a high proportion of small individuals. The opposite is true for the alternative strategy.

Population size structure is particularly important for recreationally valuable fish stocks such as largemouth bass (*Micropterus salmoides*) in North America. Angling effort for largemouth bass in North American was estimated to be 171 million angler days in 2011 (U.S. Department of the Interior, Fish and Wildlife Service 2012). Size structure of a largemouth bass stock dictates fishery catch rates and size composition, which is of particular importance to this economically important fishery that places a high value on large fish. Understanding factors that influence largemouth bass size structure could help better manage these stocks for larger fish. In Alabama, largemouth bass stocks support a valuable recreational fishery with angling effort estimated over 4.9 million angler days (U.S. Department of the Interior, Fish and Wildlife Service 2012). Statewide declines in catch rates of fish greater than 500 mm in the late 1990s and early 2000s due to outbreaks of largemouth bass virus (LMBV; Maceina and Grizzle 2006) raised questions regarding factors influencing the size structure of largemouth bass stocks in Alabama reservoirs. Two popular largemouth bass fisheries, Tennessee River impoundments Guntersville and Wheeler reservoirs, followed the statewide declines. Since the declines, statewide and Guntersville catch rates have returned to historical norms, while Wheeler average catch rates have persisted in the bottom 40% of Alabama reservoirs (Abernethy 2012). It remains unclear if between-lake differences in size structure are related to variation in growth or mortality alone, or if there is covariation in growth, mortality, and age-at-maturity within and between Guntersville and Wheeler that is consistent with life history theory.

The objective of this study was to understand factors affecting size structure of largemouth bass populations at Lake Guntersville and Wheeler Reservoir, Alabama. More specifically, my goals were to 1) document differences in size structure between the two lakes, 2) evaluate growth as a potential explanation for size structure differences by fitting growth models and assessing body condition, consumption, and diet composition, 3) test the hypothesis that differences in size structure between lakes was consistent with life history trade-offs by estimating mortality rates, quantifying associations between natural mortality and early-growth rates within and between the two populations using a catch curve analysis, and estimating length and age-at-maturity for the two populations, and 4) explore the sensitivity of between-lake differences in relative abundance of 500-mm and larger largemouth bass to changes in growth parameters, natural mortality, fishing mortality and fishing regulations.

Methods

Study Area

Lake Guntersville and Wheeler Reservoir are adjacent reservoirs on the Tennessee River in northern Alabama. Guntersville and Wheeler reservoirs are similar in size at 27,142 ha and 27,478 ha respectively, but differ in average depth, aquatic macrophyte coverage, and the magnitude of winter water level drawdown. Lake Guntersville is primarily a shallow, vegetated habitat, while Wheeler Reservoir is primarily rocky, bluff habitat. Lake Guntersville has a mean depth of 4.50 m, mean annual water level fluctuation of 0.6 m and an average aquatic plant coverage of 6,353 ha from 2010 to 2014 (Lakin; Tennessee Valley Authority, unpublished data). Wheeler has a mean depth of 4.79 m, mean annual fluctuation of 1.8 m and has an estimated average aquatic plant coverage of 283 ha from 2010 to 2014 (Lakin; TVA unpublished data). Due to the riverine nature of upstream sections of each lake, all sampling conducted on Lake Guntersville was downstream of Crow Creek and Wheeler Reservoir sampling was downstream of Lemon Slough, where the vast majority of the reservoir surface area was concentrated.

Size Structure, Growth, and Condition

Electrofishing sampling events on Guntersville and Wheeler reservoirs occurred in April of 2013 and 2014 to collect largemouth bass for ageing in adherence with the Alabama Department of Conservation and Natural Resources (ADCNR) standardized sampling protocol described in the Reservoir Management Program Manual for Alabama (Cook 1999). Spring electrofishing surveys were conducted using 7.5 GPP Smith Root electrofishing boats. Ten one-mile long transects stratified by area of the reservoir (e.g. lower, middle, upper) were randomly selected. Transects were sampled for 30 minutes each for a total effort of 5 hours per reservoir per year. Ten fish per 10 mm group were kept for aging in April 2013, and all largemouth bass were kept in April 2014. Sampling effort was tripled to thirty 30-minute transects in April 2014 to increase sample sizes.

All largemouth bass collected from age samples were measured (nearest mm), weighed (nearest g), and sex was recorded. Saggital otoliths were removed and sectioned using a low speed diamond bladed saw (South Bay Technology Model 650) following the methods described by Boehlert (1985), mounted to slides, and aged using immersion oil for clarity. Ages were estimated by two independent readers.

Length-frequency histograms of spring age samples and the proportional stock densities of preferred, memorable and 500 mm individuals (PSD-P, PSD-M, PSD-500; Anderson 1976) were used to assess size structure differences between Guntersville and Wheeler reservoirs.

Mean length-at-age was calculated using methods described by Bettoli and Miranda (2001), which corrects for biases resulting from aging subsamples of fish taken on fixed length intervals. Differences in mean length-at-age between lakes were tested with t-tests along with the Bonferroni correction for multiple comparisons. Von Bertalanffy growth models (Bertalanffy 1938) were used to model mean fish length as a function of age for each sex. Differences in growth parameters ($L\infty$, K, t0) between lakes were tested with multi-model comparison using AIC_c corrected for small sample size. Body condition was evaluated using relative weight (Anderson and Neumann 1996) and the largemouth bass standard weight equation (Henson 1991). Differences in relative weight across seasons, fish size, and between lakes was tested using ANOVA.

Consumption and Diet Composition

April 2013 age sample transect locations were fixed for a series of 15 revisits over 2 years to assess consumption, diet composition, and fish condition (i.e., relative weight). Samples from March through May were considered spring, June through September were considered summer, October through November were considered fall, and December through February were considered winter. Lengths and weights of largemouth bass were recorded to calculate relative weights. Stomach contents were removed with acrylic tubes (White 1930), with the addition of forceps, water, and suction to aid removal of large and small prey items. Van Den Avyle & Roussel (1980) reported 100% removal of stomach contents for 265 of 266 black bass using this method. Stomach contents were sorted, identified to the lowest taxon possible, counted, blotted dry, and wet weighed. For analysis, diet items were grouped into categories shad (i.e., threadfin or gizzard shad, *Dorosoma spp.*), *Lepomis spp.*, crayfish, insects, largemouth bass, and other. From these data, proportion by weight (W_i; Garvey and Chipps 2012) was calculated and variability in W_i of diet types was evaluated across seasons and fish size, and between lakes. For each 25 mm length interval, an index of consumption was calculated as the total weight of stomach contents divided by the total fish weight (PBW). Variability in PBW was evaluated across seasons, fish length intervals, and between lakes.

Mortality and Life History Tradeoffs

To assess differences in total mortality between largemouth bass at Guntersville and Wheeler reservoirs, catch curve analysis was conducted on spring age sample data. The basic catch curve model is as follows:

$$\ln(N_a) = \ln(N_0) - Z,$$

where $\ln(N_a)$ is the natural logarithm of the number of fish at each age that was captured, $\ln(N_0)$ represents the intercept, and Z equals the instantaneous rate of total annual mortality at age a. Catch curve analysis assumes constant recruitment, constant survival, and that the data are representative of the true age structure (Van Den Avyle and Hayward 1999). Analysis included maximum catch-at-age as the first age and continued until catch-at-age was less than 5 individuals.

A similar, but more complex analysis was performed using April 2014 spring age sample data to assess associations between natural mortality and first-year growth. Individuals were divided into fast, medium and slow growth types. Fish growth type (fast, medium, or slow) was determined from back-calculated lengths-at-age 1. Back-calculated lengths were estimated using the direct proportion method (Le Cren 1947). Fish with back-calculated length-at-age 1 that exceeded the 66th percentile of pooled (across lake and sex) back-calculated age-1 lengths were considered fast-growing. Individuals within the 33rd and 66th percentile were assigned to the medium-growing category, and fish in the bottom 33rd percentile were placed in the slow-growing group. Mean length-at-age was calculate for each lake, sex, and growth type combination. Despite fish being grouped into categories, growth type was described as the mean length-at-age 1 and treated as a continuous covariate in the model. A multi-model comparison with AIC was used to assess relationships between natural mortality rate and lake, sex, and growth type. Parameters that were estimated were fishing mortality rate (F), length-based sampling vulnerability, catch scaling parameters (intercepts) for each lake, and coefficients that allow M to deviate from an assumed baseline value as a function of lake, sex, and growth type. Lake and sex effects were categorical and additive, while the growth type effect was treated as a continuous, linear effect on M. Size-based vulnerability to fishing mortality was assumed based on the estimated proportion of fish exceeding the minimum length limit at each reservoir given a cumulative normal distribution around the mean length-at-age with a coefficient of variation (CV) of 0.15. Fishing mortality of fully vulnerable fish was held constant across ages. Size-based vulnerability to sampling (S_vuln_a) was assumed to be sigmoidal in shape:

$$S\_vuln_a = 1 / (1 + e^{(-h^* (l_a - l_{50}))})$$

where l_a is the mean length-at-age, l_{50} is the estimated length at 0.50 sampling vulnerability and h was the estimated steepness parameter. A baseline natural mortality rate from an average of Pauly (1980), Hoenig (1983), and Jensen (1996) was assumed for medium-growing Lake Guntersville females as an arbitrary reference group. The baseline M for the reference category was a necessary assumption because of confounding affects between fishing and natural mortality in the catch curve model. Deviations between all other group-specific (i.e., lake, sex, growth type combinations) M values and the assumed baseline value were modeled as a function of growth type, lake, and sex by fitting a series of models that represented different assumptions for these relationships. Relative empirical support across models was evaluated using AIC. For example, AIC differences between models that allowed M to vary as a function of growth type vs. models that assumed growth type invariant M were used to test for associations between M and first-year growth. AIC was also used to assess whether there was support for differences in F between lakes. Growth type, lake and sex specific M were derived from parameter estimates. Lake specific average M was calculated by taking the weighted average of the growth type and sex specific M estimates for each lake, weighted by sample relative abundance. This approach assumes that the M of each covariate combination contributes to the total lake M proportionally with the contribution of the sample size. To assess the sensitivity of model estimates to assumptions, the analysis was repeated under assumed baseline M values ranging from 0.264 to 0.469.

Maturity

During the 2014 spring age sample, ovaries were removed from a subsample of 10 female largemouth bass per 10 mm length bin from 200 mm to 400 mm from each lake for gonad histology to estimate length and age-at-maturity. Samples were trimmed, preserved in formalin, dehydrated, cleared, and infiltrated with paraffin wax following standard histological techniques (Hinton 1990). Gonads were sectioned with a microtome at 5 um, placed on glass slides, and stained with hematoxlyin and eosin (Hinton 1990). Female ovary samples were observed under a compound microscope at 40x and classified into 6 maturity stages (i.e., primary growth, early secondary growth, vitellogenesis, final oocyte maturation, atresia, and spent) based on the most mature stage present in each ovary sections (James 1946; Kelley 1962; Gran 1995; Grier et al.

2009). Females in vitollogenesis or later stages were categorized as mature. Logistic regression and multi-model comparison using AIC was used to estimate differences in maturation schedules (i.e., length and age-at-maturity) between Guntersville and Wheeler reservoirs in 2014.

Simulation Modelling

An age-structured equilibrium model was used to assess which life history parameters most strongly influenced between-lake differences in the potential for an individual fish to reach 500 mm. Assumed sex-specific growth, M, and constant F parameters were based upon estimated and derived parameters from the 2014 catch curve analysis model. Vulnerability to fishing mortality at age (F_vuln_a) was the probability of an individual fish to be above the minimum length limit, calculated from a normal distribution around the mean length-at-age assuming a standard deviation of 0.15. Survivorship (i.e., probability of surviving from age 1 to a given age) was calculated as:

$$l_a = e^{-F*F_{vuln_a}-M*(a-1)}$$

Where l_a was survivorship to age a, F was instantaneous fishing mortality rate, F_vuln_a was the age-specific vulnerability to fishing, and M was instantaneous natural mortality. The probability of an individual fish to be greater than 500 mm at a given age ($p500_a$) was calculated from a normal distribution around the mean length-at-age a from the given lake and sex assuming a standard deviation of 0.15. The predicted lifetime probability for an individual recruit to both survive to age a and exceed 500 mm total length was:

$$\varphi 500 = \sum_a l_a * p500_a$$

Sex-specific φ500 was averaged and compared between lakes as a ratio of Lake Guntersville φ500 relative to Wheeler Reservoir φ500 (φ500 ratio) given lake and sex specific growth parameters estimated from the Von Bertalanffy growth model.

A sensitivity analysis was performed to indicate which parameters (e.g., growth, M, F, or minimum length limit) had the greatest influence on per recruit probability to survive to 500 mm, and which could explain between-lake differences in size structure. Sensitivity was calculated by varying M, F, and MLL by 10% under three scenarios of assumed M and evaluating the change in φ500 ratio. The sensitivity analysis was run under three scenarios of assumed M. Further scenarios were run to replicate the observed ratio of fish greater than 500 mm. First, M was allowed to differ between lakes and sexes based on the estimates derived from the 2014 catch curve analysis model. Additional scenarios included Wheeler MLL was set to 0 mm rather than 304 mm, F was set to twice the assumed F, and Wheeler Reservoir F was set 1.5 times Lake Guntersville F.

Results

Size Structure, Growth, and Condition

In spring 2013 I collected 313 and 371 largemouth bass from Guntersville and Wheeler reservoirs, respectively. Length-frequency distributions indicate a higher PSD-P, PSD-M, and PSD-500 at Lake Guntersville relative to Wheeler Reservoir (Figure 1). Largemouth bass that exceeded 500 mm contributed 5.27% of the spring electrofishing samples at Lake Guntersville and 2.60% at Wheeler Reservoir. During spring samples, 2.03 times more largemouth bass greater than 500 mm were sampled at Lake Guntersville than Wheeler Reservoir. Wheeler Reservoir female mean length at age was significantly greater than Lake Guntersville at ages 1 (df=107, t=4.95, p=2.75e-6) and 2 (df=28, t=2.39, p=0.024) and Wheeler Reservoir male mean length at age was significantly greater at ages 2 (df=98, t=1.98, p=0.050), 3 (df=25, t=2.75, p=0.011), and 4 (df=19, t=2.14, p=0.025; Figure 2). Multi-model comparison using AICc supported no difference in female growth parameters between lakes, but a greater K for males at Wheeler Reservoir relative to Lake Guntersville (Figure 3; Table 1; Table 2).

In spring 2014 I collected 840 and 392 largemouth bass from Guntersville and Wheeler reservoirs, respectively. Wheeler Reservoir female mean length at age was significantly greater at ages 2 (df=133, t=2.58, p=0.011), 3 (df=130, t=3.48, p=6.74e-4), 5 (df=32, t=3.32, p=0.002) 6 (df=28, t=2.32, p=0.028), and 8 (df=10, t=2.98, p=0.013) and Wheeler Reservoir male mean length at age was significantly greater at ages 2 (df=131, t=3.21, p=0.002) and 4 (df=74, t=2.90, p=0.005; Figure 4). Lake Guntersville female mean length at age was significantly greater at age 9 (df=13, t=4.19, p=9.83e-4). Multi-model comparison suggested greater female $L\infty$ and K for Wheeler Reservoir relative to Lake Guntersville as well as shorter male $L\infty$ and greater K for Wheeler Reservoir relative to Lake Guntersville, but with high uncertainty (Figure 5; Table 1; Table 2).

Average relative weight (Wr) of Lake Guntersville and Wheeler Reservoir largemouth bass was 97.74 and 96.90, respectively. Lake Guntersville largemouth bass Wr was significantly greater than Wheeler Reservoir largemouth bass on average (df=1, F=8.95, p=0.0028), but the difference in mean Wr was small at 0.96. Differences in Wr between lakes were not significant within season except in fall (p=0.0004). There were no clear patterns in relative weight between lakes across length groups or season (Figure 6).

Consumption and Diet composition

A total of 747 and 1022 diet samples were collected from Guntersville and Wheeler reservoirs over the course of 15 sampling events. Major diet items consisted of shad, *Lepomis spp.*, crayfish, aquatic insects, terrestrial insects, largemouth bass, silversides, golden shiners, shrimp, other fish, and unidentifiable fish. In general, shad was the primary diet item of Wheeler

Reservoir largemouth bass while Lake Guntersville largemouth bass diets containted a higher proportion of *Lepomis spp.* and were more diverse (Figure 7, 8). When comparing proportion by weight (Wi), shad made up the majority of Wheeler Reservoir diets during all seasons for fish both greater and less than 300 mm. *Lepomis spp.* made up the majority of Lake Guntersville diets for fish less than 300 mm in spring and winter while shad made up the majority in fall. Lake Guntersville diets were more diverse during the summer with shad, *Lepomis spp.* and insects all making up similar proportions of the diet. Diets of Lake Guntersville fish greater than 300 mm primarily consisted of *Lepomis spp.* in the spring, fall and winter, and shad in the summer.

Average PBW did not significantly differ between Guntersville and Wheeler reservoirs (df=1, f=3.29, p=0.0697). Differences in PBW between lakes were not significant within any season except in fall, where Lake Guntersville PBW was greater than Wheeler Reservoir PBW. There were no clear patterns in consumption between lakes across length groups or season (Figure 9).

Mortality and Life History Tradeoffs

The 2013 catch curve estimated a total annual mortality (A) for Lake Guntersville largemouth bass of 28% (Z=0.328; $r^2 = 0.60$) with a maximum age of 13 years. Total annual mortality at Wheeler Reservoir was 40% (Z=0.513; $r^2 = 0.90$) with an observed maximum age of 9 years. (Figure 10).

Predicted catch-at-age from the 2014 catch curve model reasonably fit the observed catch-at-age data. Generally the model under-predicted catch-at-age for ages 2-4 for fast growers and over-predicted catch-at-age for the oldest ages for fast growers. The analysis revealed that growth type (back-calculated length at age 1) was positively related with M and multi-model comparison showed that growth type was a better predictor of M than sex or lake. The top four models all included growth type as a covariate while the bottom four did not (Figure 11, 12; Table 3). Maximum age of fast growers was less than that of slow growers, which also suggests a higher M. The sex effect suggesting males have lower M relative to females of a given growth type and the lake effect suggesting Wheeler Reservoir has greater M relative to Lake Guntersville did not significantly improve model fit. Derived estimates of M demonstrated the lake, sex, and growth type effects (Figure 13). Instantaneous natural mortality rate for fast, medium, and slow growing Lake Guntersville females was 0.435 yr^{-1}, 0.367 yr^{-1}, and 0.297 yr^{-1}, and were derived as a function of mean back-calculated length-at-age 1. Mean back-calculated length-at-age 1 was 214 mm for fast growers, 170 mm for medium growers, and 126 mm for slow grower. The proportion of largemouth bass in each of the growth types differed between lakes and sexes (Table 4). The Lake Guntersville sample had a higher proportion of slow growers relative to Wheeler Reservoir and males had a higher proportion of slow growers than females. Total natural mortality derived from the 2014 sample proportions was 0.369 for Wheeler Reservoir and 0.337 for Lake Guntersville.

When the model was run under a range of assumed baseline M values for the reference category, model selection conclusions did not change (Table 3). As the assumed baseline M increased, model averaged estimates of F and C decreased while h and L_{50} increased. The sex and lake effect sizes increased at high M and at low M (Table 5).

Maturity

In spring 2014 a total of 175 and 130 female largemouth bass ovary samples were taken from Guntersville and Wheeler reservoirs, respectively. Forty-one of 175 Lake Guntersville females and 31 of 130 Wheeler Reservoir females were immature. Logistic regression estimated length at 50% mature (L_{50}) to be 227 mm at Lake Guntersville and 235 mm at Wheeler Reservoir

(Figure 14), and age at 50% mature (A_{50}) to be 1.50 years at Lake Guntersville and 1.62 years at Wheeler Reservoir (Figure 15). Multi-model comparison using AIC suggested no between-lake difference in maturity as a function of length, but there was AIC support for differences in maturity as a function of age (Table 6). The proportion of age 1 largemouth bass that were mature was greater at Lake Guntersville but the proportion of age 2-3 largemouth bass that were mature was greater at Wheeler Reservoir because of the steeper ascent of the curve at Wheeler Reservoir.

Simulation Modelling

Given the growth parameters estimated from the 2014 age sample and a constant mortality between lakes and sexes derived from an average of the catch curve model, the life time per recruit expectation of a female largemouth bass reaching 500 mm ($\varphi 500$) was 0.308 at Lake Guntersville and 0.325 at Wheeler Reservoir. Male age-1 recruits had a $\varphi 500$ of 0.175 at Lake Guntersville and 0.199 at Wheeler Reservoir. The ratio of $\varphi 500$ of Lake Guntersville relative to Wheeler Reservoir was 0.915. Thus, the model suggested an individual largemouth bass recruit from Wheeler Reservoir had a higher probability of reaching 500 mm than an individual from Lake Guntersville. The per recruit model output was more sensitive to changes in M than to changes in F and MLL, and this conclusion was consistent across a range of M (Table 7). A 10% increase in Wheeler Reservoir M elicited an increase of the $\varphi 500$ ratio from 0.915 to 0.917 ($\Delta = 0.002$). The $\varphi 500$ ratio was insensitive to a 10% increase in Wheeler Reservoir F ($\Delta = 1e\text{-}4$) and 10% decrease in Wheeler Reservoir MLL ($\Delta = 2e\text{-}5$). Allowing M to differ using derived estimates of M from the 2014 catch curve analysis elicited the greatest response with an increase of the $\varphi 500$ ratio from 0.915 to 1.102 ($\Delta = 0.186$). The $\varphi 500$ ratio was insensitive to decreasing Wheeler Reservoir MLL to 0 mm ($\Delta = 0.002$). The $\varphi 500$ ratio was insensitive to variation in the magnitude of F at Wheeler Reservoir relative to Lake Guntersville ($\Delta = 0.012$). Increasing Wheeler Reservoir F to 1.5 times Lake Guntersville F increased the $\varphi500$ ratio to 0.962 ($\Delta = 0.047$; Table 7). These conservative assumptions further supported that differences in M likely drive the observed difference in size structure between lakes.

Discussion

My analysis suggests that largemouth bass populations at Guntersville and Wheeler reservoirs differ in terms of size structure, early growth, natural mortality, and possibly maturity. Wheeler Reservoir had a lower proportion of largemouth bass greater than 500 mm than Lake Guntersville, and fish at Wheeler Reservoir were somewhat longer-at-age relative to Lake Guntersville, particularly early in life. This was reflected in a higher proportion of fish exhibiting fast and medium growth types at Wheeler Reservoir than Lake Guntersville. Life history theory would predict that these fast growing largemouth bass would suffer higher mortality. The 2014 catch curve analysis supported that prediction. The growth type effect being present in the top models and the lack of support for a substantial lake effect suggests that differences in M can be explained by length-at-age 1 rather than a lake effect. Attempts have been made to quantify the relationship between growth, mortality, and other variables to predict natural mortality rates (Pauly 1980; Hoenig 1983; Myers and Doyle 1983; Jenson 1996). A relationship between length-at-age 1 and mortality was first explored when Lee (1912) discovered that the back-calculated lengths of older fish were less than the present mean lengths at age, suggesting that the fastest growing individuals in a population did not survive to make up a large proportion of the older fish. This was attributed to faster growing individuals being susceptible to fishing mortality earlier than slow growing individuals rather than a life history trade-off. My catch curve analysis was an attempt to model the life history trade-off by accounting for a positive relationship between M and early growth, a positive relationship between F and early growth described by

Lee’s Phenomenon, and also size-selective fishing and sampling vulnerability. Life history theory would also predict earlier age-at-maturity and the same size-at-maturity at Wheeler Reservoir relative to Lake Guntersville in order to optimize reproductive fitness. Age at 50% maturity was higher at Wheeler Reservoir although the ascent of the maturity curve was steeper, making strong conclusions about differences in maturity between reservoirs difficult. More samples, in smaller length intervals, including more immature individuals is necessary to better define the maturity curves and detect differences in maturity between the two populations.

There are many hypothesis for the cause of a relationship between growth and mortality such as behavior, inefficient metabolic function, somatic development, and immune function (Mangel and Stamps 2001). Faster growing individuals may be inherently more aggressive and more susceptible to predation (Metcalge and Frazer 1997; Dunham et al. 1999). At a cellular level, dividing and growing cells cannot perform at peak efficiency (Arendt 2000) and damage by free radicals produced as byproducts of aerobic metabolism could accumulate to cause death (Hartman 1956). Faster growing individuals may also be more susceptible to developmental inefficiencies. For example, fast-growing salmon are more likely to develop coronary arterial lesions than slower growing individuals (Saunders et al. 1992). My data cannot indicate the cause for growth-natural mortality associations within these populations but more detailed experimental work is needed to ascertain specific mechanisms for higher natural mortality rates for largemouth bass that attain a larger total length at age 1.

The trade-offs between life history parameters are dictated by environmental constraints (Winemiller and Rose 1992); however, the specific selective forces that may have caused the life history plasticity between these populations are still unknown. Wheeler Reservoir largemouth bass consumed a higher proportion of fish by weight than Lake Guntersville largemouth bass.

Furthermore, Wheeler Reservoir largemouth bass ate a higher proportion of shad relative to the calorically less beneficial *Lepomis spp.* (Wright and Kraft 2012) than did Lake Guntersville largemouth bass. Variation in diet composition or consumption rate can influence growth (Shelton et al. 1979; Timmons et al. 1980; Keast and Eadie 1985; Bettoli et al. 1992). Bettoli et al. (1992) found an increase in age 0 largemouth bass growth rates at Lake Conroe, Texas after reductions in macrophyte density which was attributed to earlier shifts to piscivory. The magnitude of variation in macrophyte density that resulted in faster growth in Bettoli et al. (1992) exists between Wheeler and Guntersville reservoirs (Tennessee Valley Authority; unpublished). There is further evidence suggesting that macrophyte density influences growth in largemouth bass (Glass 1971; Crowder and Cooper 1979; Wrenn et al. 1996; Brown and Maceina 2002). Wrenn et al. (1996) and Brown and Maceina (2002) found differences in young-of-year largemouth bass growth between high and low macrophyte density at Lake Guntersville and Lake Seminole, Georgia, respectively. It is possible that the difference in size structure between Guntersville and Wheeler reservoirs in response to differences in life history strategy may be related to habitat and diet. Another possibility is genotypic differences between largemouth bass populations at Guntersville and Wheeler reservoirs. Preliminary findings from a concurrent study of largemouth bass genetics at these two reservoirs suggests that a higher proportion of Florida largemouth bass (*Micropterus salmoides floridanus*) alleles are present in largemouth bass caught at Lake Guntersville than Wheeler Reservoir (S. Gowan, Auburn University, personal communication) despite historical stocking of Florida largemouth bass into both lakes. A genotypic difference could explain differences in life history strategy and the higher proportion of slower growing, longer living largemouth bass at Lake Guntersville.

There are several important caveats to consider when interpreting the findings of this analysis. Sex determination was uncertain for some age 1 largemouth bass. Gonadal development of small, immature largemouth bass is limited, which makes sex determination difficult. Misassignment of age 1 largemouth bass sex may have influenced the sex specific catch at age distributions. Catch-at-age 1 within the 2014 catch curve influences sampling vulnerability estimates at early ages and has little influence on mortality estimates. In addition, different combinations of sex and growth type within a lake all should have experienced the same year-class strength. The model does not account for this variation in year-class strength. Extreme year-classes could introduce bias in the magnitude of the mortality estimates and the lake effect but not in the effect of the covariates sex and growth type. A strong year-class at older ages, such as the age 7 year-class present at Lake Guntersville, could underestimate mortality and overestimate the lake effect on M. The final caveat is that the model estimated that largemouth bass M was greater for females relative to males. This does not seem biologically rational unless there are differences in F or catch-and-release mortality between sexes that have not been incorporated into the model.

The simulation modeling was a deterministic model and the sensitivity analysis was an attempt to quantify the influence of M, F, and MLL on individual lifetime survivorship to 500 mm in order to understand what factors most influenced size structure in a population. Despite the simplicity of the model, it gives insight into the fact that M likely has a greater influence on size structure relative to F and MLL and that variation in growth between Guntersville and Wheeler reservoirs alone cannot explain the difference in size structure. The analysis was not able to reproduce the observed ratio of 500 mm largemouth bass for the two reservoirs because growth and derived mortality estimates did not differ enough between reservoirs. A caveat of this simulation model is that year-class strength was not accounted for within the analysis. In medium to large impoundments, year-class strength is likely to have more influence on size structure than either growth or mortality (Carline et al. 1984). Explaining the variation in catch-at-age with recent differences in year-class strength within the model could help reproduce the observed ratio of 500 mm largemouth bass for the two reservoirs. Further research to estimate recent year-class strengths should be explored to explain size structure differences between Lake Guntersville and Wheeler Reservoir. More extensive maturity sampling could also further support life history plasticity between these two populations.

III. Largemouth bass recruitment and mortality at three Alabama Reservoirs estimated with catch-at-age analysis

Abstract

Obtaining reliable estimates of year-class strength and fishing mortality is essential to understanding factors affecting temporal variability in stock abundance, anticipating population trends, and helping managers make informed decisions. Statistical catch-at-age analysis (SCAA) is a useful tool for estimating parameters of interest from a time series of age composition and catch rate data sets. This method has yet to be applied to freshwater fisheries with important recreational value such as largemouth bass (*Micropterus salmoides*) stocks. I used fishery-independent survey age/length composition and catch-per-effort data from largemouth bass stocks at three Alabama reservoirs, to reconstruct a time series of year-class strength, annual fishing mortality rates, and survey vulnerability schedules, then performed a sensitivity analysis under a variety of model assumptions. Model estimates of year-class strength and temporal trends in fishing mortality were robust to changes in assumptions about effective sample size, natural mortality rate, and temporal variability in fishing mortality. However, the magnitude of instantaneous fishing mortality rates were unrealistically high and sensitive to model assumptions. Year-class strength estimates were correlated among lakes to demonstrate possible management implications and correlations were weak. Our application of SCAA to survey datasets routinely collected by management agencies for largemouth bass potentially provides a comprehensive approach to estimating year-class strength for these stocks without increasing sampling effort, but future investigations of the utility of SCAA for these stocks should assess the potential for bias in the magnitude of fishing mortality estimates.

Introduction

Estimating year-class strength and fishing mortality rates are central goals of fish stock assessments because variation in these quantities affects stock abundance and size structure.

Variation in year-class strength has long been recognized as strongly affecting stock abundance and size structure (Carline et al. 1984; Maunder and Deriso 2003). Estimates of year-class strength can be used to test hypotheses regarding factors that influence recruitment variation (Maceina 1997). Moreover, the ability to predict year-class strength can help to forecast angler satisfaction and harvest (Colvin 1991). Reliable estimates of fishing mortality are critical to assessing the current stock status with respect to target and limit reference points and determining the value of harvest regulations (Hightower et al. 2001). In addition, variation in fishing mortality across sizes or ages can alter size structure by increasing the exploitation of particular size (age) classes of fish while protecting others (Wilde 1997; Allen et al. 2008), and overall changes in exploitation rate can influence stock abundance (Hutchings and Myers 1994; Pauly et al. 2002; Baum et al. 2003).

Much research has been dedicated to developing statistical assessment methods to estimate year-class strength and fishing mortality rates from commonly available data such as age composition information (Fournier 1990 et al.; Maunder and Watters 2003; Porch et al. 2006), but these methods are often challenged by the confounding effects of natural mortality, fishing mortality, and recruitment on age-specific catches (Hilborn and Walters 1992; Quin and Deriso 1999). The simplest age-based stock assessment model to estimate year-class strength and fishing mortality is the catch curve, a linear regression of the natural log of catch against age. The slope of the regression is interpreted as an estimate of the instantaneous total mortality rate (Z), and instantaneous fishing mortality rate (F) can be estimated by subtracting M from Z assuming a constant instantaneous natural mortality rate (M; i.e., $Z = F + M$). The catch curve can be fit on a calendar year basis to different cohorts of fish that are different ages, or it can also be fit on a cohort basis by tracking catch-at-age of individual cohorts across multiple consecutive annual samples.

For freshwater recreational fisheries, year-class strength and instantaneous fishing mortality rates are typically estimated via an annual catch curve that is fit on a calendar year basis. These models are usually fit to catches-at-age from annual fishery-independent surveys such as standardized electrofishing transects, gill nets, or trap nets. Examples of these analyses are numerous and have been applied to largemouth bass and crappie (Maceina 1997; Maceina and Bettolli 1998; Sammons et al. 2002). Year-class strength can be estimated from these models by assuming residuals from the catch curve represent recruitment variation (Maceina 1997; Maceina and Bettolli 1998; Sammons et al. 2002).

Annual catch curves can provide reliable estimates of year-class strength when assumptions are satisfied (Maceina 2004; Catalano et al. 2009), but they suffer from several potential short-comings. They are typically applied to one calendar year of catch-at-age at a time because there are often not sufficient consecutive years of surveys to run the model on individual cohorts. Thus estimates of year-class strength are informed by one data point per cohort (one residual per age class) and samples often consist of few age classes (<10). Young fish are excluded from the analysis because they are not fully vulnerable to the sampling gear, and the oldest age classes are sometimes excluded because of low sample size, further truncating an already data limited analysis. Fewer age classes result in each age class having more influence on instantaneous total mortality rate estimates and thus residuals. The assumptions of a catch curve include constant mortality over time and across ages, constant recruitment, and the population is closed to other populations. When these assumptions are violated, bias is introduced into the estimates because catch-at-age is confounded by year-class strength, instantaneous natural mortality rate, and instantaneous fishing mortality rate (Hilborn and Walters 1992; Quin and Deriso 1999). Agencies that regularly perform this analysis typically have regular standardized sampling programs (Cook 1999), thus the data often exist to develop more comprehensive modelling approaches that make use of the entire time series of survey catch-at-age data.

A method often used to estimate parameters of interest in commercial fish stocks is a statistical catch-at-age analysis (SCAA; Fournier 1990 et al.; Maunder and Watters 2003; Porch et al. 2006). This technique uses multiple annual fishery dependent and independent datasets in a holistic, interconnected approach (Maunder and Watters 2003; Porch et al. 2006). Use of a SCAA model structure is pervasive in marine fisheries assessments (Maunder and Punt 2014) and commercially important freshwater stocks (Vandergoot et al. 2011), but to date, has not been applied to freshwater stocks with important recreational fisheries. The SCAA approach could provide a useful platform for combining often discontinuous annual fishery-independent surveys from freshwater fisheries into a single analysis because of the linked nature of the model. Thus, using SCAA on recreational fish stocks has the potential to be a powerful tool that uses all of the data available rather than a single calendar year analysis that does not include all other years of information as is done with the annual catch curve. Flexibility of the SCAA allows for multiple types of data inputs (i.e., multiple survey catch rate series, catch-at-age, creel survey, mark-recapture) to estimate a variety of parameters of interest such as time series of year-class strength and instantaneous fishing mortality rates. Estimating trends in year-class strength and relative changes in instantaneous fishing mortality rate over time can help explain variation in abundance and size structure, and estimates of year-class strength can also be correlated with environmental variables or with other stocks to explain variation in year-class strength. One potential limitation for the application of SCAA to recreational fisheries could be the common lack of age specific harvest and effort data for these fisheries due to the expense of collecting this information. However, Porch et al. (2006) developed an SCAA model for goliath grouper (*Epinephelus itajara*), known as the “catch free” SCAA model, that can be fit only to survey age composition and catch rates thereby eliminating the need for fishery-dependent data and potentially enhancing the applicability of the method for freshwater recreational fisheries.

Largemouth bass is one of the most popular recreational sport-fish species in North America. Year-class strength trends are often of great interest to scientists, managers, and anglers of these fisheries. Catch curves have been used to explore year-class and mortality trends for these stocks, but assessment of largemouth bass fisheries could benefit from the more rigorous approach provided by SCAA. The SCAA model has yet to be applied in the assessment of largemouth bass populations. In Alabama reservoirs, the Alabama Department of Conservation and Natural Resources (ADCNR) routinely collects age structure and catch rate (CPE) data via spring electrofishing surveys, which provides an opportunity to explore the application of SCAA to these data. The objective of this study is to 1) fit SCAA to reconstruct year-class strength and fishing mortality time series using age composition and relative abundance data from three Alabama reservoirs (Demopolis Reservoir, Lake Guntersville, and Wheeler Reservoir) which vary in terms of sampling frequencies, largemouth bass size structure, and habitat, 2) conduct a sensitivity analysis of the SCAA model under a variety of scenarios that differ in data inputs, assumed natural mortality, temporal variation in fishing mortality, and 3) correlate annual year-class strength estimates from the SCAA among reservoirs to demonstrate possible management implications.

Methods

Study Area

The SCAA model was applied to data from three Alabama reservoirs: Demopolis, Guntersville, and Wheeler reservoirs. Demopolis Reservoir is an impoundment of the Black Warrior-Tombigbee waterway in Marengo County. Lake Guntersville and Wheeler Reservoir are adjacent reservoirs on the Tennessee River in northern Alabama. Guntersville and Wheeler reservoirs are 27,142 ha and 27,478 ha respectively. Lake Guntersville is primarily located in Jackson and Marshall counties and the majority of Wheeler Reservoir is located in Lawrence and Limestone counties. Demopolis Reservoir has been sampled on a nearly annual basis, Lake Guntersville roughly every 2 year, and Wheeler Reservoir roughly every 3 years since the early 1990s. These three reservoirs were chosen for analysis because they have sufficiently long survey time series to follow multiple cohorts through time and samples within impoundments were collected using consistent methods. Varying sampling frequencies (i.e., proportion of years with a sample) across reservoirs as well as the availability of supplemental electrofishing survey CPE data from Guntersville and Wheeler reservoirs collected by the Tennessee Valley Authority (TVA) allowed us to explore model performance under varying sampling frequency and inclusion of additional data sets.

Data Input

Datasets used in the SCAA consisted of fishery independent age proportion and catch-per-effort (CPE; largemouth bass captured per hour of electrofishing) data collected by the ADCNR via spring electrofishing using standardized sampling protocols (Cook 1999). Spring electrofishing surveys were conducted using an 18-foot aluminum boat outfitted with a 7.5 GPP

Smith Root electrofishing unit. Electrofishing samples were collected at ten random 30-minute transects stratified by area of the lake (e.g. lower, middle, upper). Ten largemouth bass per 25 mm length group were kept for aging and age-length proportions were used to project ages to unaged fish (i.e., an age-length key). Supplemental electrofishing CPE datasets collected by the TVA were available for Guntersville and Wheeler reservoirs from 2002 to 2011. TVA data were collected using 7.5 GPP Smith Root electrofishing boats via twelve 30-minute spring electrofishing transects for 3 to 4 creeks per reservoir. The creeks were within the same sampling area of ADCNR surveys and did not change over time; however, effort was reduced from 4 to 3 creeks after 2006.

Model Structure

The SCAA model estimated annual relative year-class strength (R_t), the annual instantaneous fishing mortality rate of fully-vulnerable age classes (F'_t), survey catchability and age-specific vulnerability, and the residual sampling variation of annual electrofishing CPE observations (i.e., standard deviation, σ_s), by fitting the model to survey age composition and CPE data sets. Cohort abundance-at-age was modeled as an exponential decline of age-1 relative recruits (i.e., year-classs strength, R_t) via the total instantaneous mortality rate (Z; Table 9.1). Estimates of R were assumed drawn from a log-normal distribution with a mean of 1.0 and standard deviation (σ_r) of 0.55 (T9.2) representing the assumed magnitude of variation in interannual recruitment variation. The estimate of σ_r was taken from a stock-recruitment meta-analysis of 54 fish stocks by Goodwin et al. (2006). The mean value of 1.0 for R_t was necessarily set because the fishery independent survey data were only informative on the relative changes in year-class strength over time and thus contained no information on the absolute scaling of recruitment (i.e., numbers of fish). Cohort abundance declined over time as a function of $Z_{a,t}$, which was a function of constant M and age and year specific instantaneous fishing mortality $F_{a,t}$ (T9.3). Instantaneous natural mortality was assumed to be constant among ages and years and derived from an average of estimates using Pauly (1980), Hoenig (1983), and Jensen (1996). Pauly (1980) estimated a relationship where natural mortality (M) was a function of growth parameters $L\infty$ (maximum asymptotic length), K (1/year), and T (^{0}C, mean annual water temperature). Jenson (1996) used life history theory to suggest that $M = 1.5$ K while Hoenig (1983) suggested a relationship between M and maximum age. Age-specific fishing mortality was modeled as the product of age-specific vulnerability to fishing (T9.4) and the instantaneous fishing mortality rate of fully-vulnerable age classes (F'_t), which was modeled as a random walk process over time (T9.5). The random walk process allowed F'_t to vary over time but constrained the interannual variation by assuming the deviations were drawn from a lognormal distribution with mean 0 and assumed interannual standard deviation (σ_f) of 0.05. This constrained F'_t within 10% of the previous year. Vulnerability describes the proportion of fish at age or length that are vulnerable to fishing or sampling gear. Age-specific vulnerability to fishing mortality was derived from the proportion of fish that exceeded the minimum length limit, which was obtained from a cumulative normal probability distribution for length-at-age. The mean of this probability distribution was the mean length-at-age estimated by fitting the Von Bertalanffy growth model (Bertalanffy 1938) to length-at-age data from all survey years, and was assumed constant across years with a coefficient of variation (CV) of 0.15. The total annual survey catch was predicted from abundance at time and age given a known sampling effort (E_y), an estimated constant catchability (q) and size-based survey vulnerability ($S_{a,s}$; T9.6). Survey vulnerability was modeled with a logistic curve, which assumes vulnerability is asymptotic and cannot decline at larger sizes (T9.7). From this, annual survey CPE (T9.8) and age proportions (T9.9) could be predicted.

Parameter estimation was achieved by minimizing the sum of the negative log-likelihoods and parameter penalties (T10.1). The model assumed a lognormal sampling distribution for survey CPE (T10.2), and a multinomial sampling distribution for survey age proportions (T10.3). An assumed weighting factor, the effective sample size (ESS), was applied to the multinomial age proportion likelihood in order to set the sampling variance of the age proportions. The ESS represents the effective number of individual fish that were examined for age determination. This value is almost always less than the true number of fish examined due to correlations inherent in age/length proportion data (Maunder 2011; Francis 2011), but is usually greater than the number of sites sampled (Pennington and Vølstad 1994). The ESS was initially set to 40 for the baseline model configuration. Additional likelihood components were computed for the interannual variation in R_t (T10.4) and the random walk in F'_t (T10.5), which were both assumed to be lognormally distributed. A penalty was added to meet an assumption that at least one age class was fully vulnerable to sampling (T10.6). Model estimates were constrained beyond reasonable values in order to improve model convergence by preventing the optimization process from attempting parameter estimates orders of magnitude greater than reasonable values and becoming caught in local minima. Standard error of parameter estimates were derived from Wald confidence intervals by inverting the hessian matrix.

Model Scenarios

To investigate model response to changes in supplemental data inputs and assumptions, the SCAA was fit under a variety of scenarios that represented a range of assumed natural mortality rates, ESS values, the magnitude of temporal variation in F'_t, and whether or not the

TVA electrofishing survey data were integrated into the Lake Guntersville and Wheeler Reservoir models (Table 11). The SCAA was fit under a baseline natural mortality assumption derived from the mean of Pauly (1980), Hoenig (1983), and Jensen (1996) and two additional scenarios being the highest and lowest estimates of natural mortality from Pauly (1980), Hoenig (1983), and Jensen (1996). I also ran a scenario in which natural mortality rate declined exponentially with increasing mean length-at-age (T9.10; Lorenzen 2000). The Lorenzen (2000) length-specific M specification was parameterized such that M declined with length. The baseline M value was reached at the length-at-maturity, which was estimated from Jensen (1996) as 0.66*L∞. The model was also fit under 3 values of ESS (20, 40, 60) and 3 values of σ_f (1.0e-10, 0.05, 0.10). ESS values of 20, 40, and 60 were chosen because the values were between the number of sites sampled (10) and the average number of fish aged across years at most of the lakes (100-150). In an effort to increase precision of parameter estimates, Guntersville and Wheeler reservoirs had another scenario in which TVA CPE data collected via spring electrofishing sampling were included as an additional negative log likelihood (T10.7). The TVA survey vulnerability was assumed identical to the ADCNR survey vulnerability, but a separate catchability (q_{tva}) parameter was estimated to accommodate the different scaling of the TVA survey CPE data. Model fit to age proportion and CPE data, as well as estimates of R_t and F'_t were compared among scenarios to understand possible influences of different assumptions about M, ESS, and σ_f on model fit and estimates.

Correlations in Year-class Strength

To demonstrate possible applications of fitting SCAA models in order to estimate R_t, I correlated baseline model estimates of R_t between lakes to investigate commonalities in year-class strength.

Results

Estimates of year-class strength ranged from lows of 0.55, 0.48, and 0.23 to highs of 1.90, 2.50, and 2.03 for Demopolis, Guntersville and Wheeler reservoirs respectively. The SCAA model suggested strong year-classes for Demopolis Reservoir in 1994, 2008 and 2009 and weak year-classes in 1995, 1998, 2004, and 2006. Strong year-classes were estimated for Lake Guntersville in 1999, and 2008 and weak year-classes in 2003, and 2006. The SCAA model suggested strong year-classes for Wheeler Reservoir in 1994, 2003 and 2007 and weak year-classes in 1995, 2004, and 2006 (Figure 16). The between lake year-class strength correlations were weak, ranging from 0.28 to 0.55, despite a shared weak year-class in all three lakes in 2006 followed by strong year-classes in 2007-2008 (Figure 16). The mean standard error of the R_t parameter estimates was 0.19, 0.24, and 0.27 for Demopolis, Guntersville and Wheeler reservoirs, respectively.

Estimates of the instantaneous fishing mortality rate were an average of 0.29 yr^{-1} at Lake Guntersville, 0.63 yr^{-1} at Wheeler Reservoir and 0.66 yr^{-1} at Demopolis Reservoir. The SCAA suggested a modest decrease in F over time at Wheeler and Guntersville reservoirs and an increase at Demopolis Reservoir (Figure 17). The mean log-scale standard errors of the F'_t estimates was 0.15, 0.26, and 0.17 for Demopolis, Guntersville and Wheeler reservoirs respectively.

Size-based survey vulnerability varied between lakes with largemouth bass become fully vulnerable to survey gear at about 200 mm, 75 mm, and 450 mm at Demopolis Reservoir, Wheeler Reservoir and Lake Guntersville respectively (Figure 18).

The SCAA model predictions were generally consistent with the observed CPE and age proportion data. The model tended to under-predict survey CPE in years with high CPE and over-predict in years of low CPE (Figure 19). The age composition data indicated strong and weak year-classes that the model could consistently track across multiple annual age composition samples. Temporal variation in CPE was generally consistent with the time series of year-class strength such that strong year-classes were followed by increases in survey CPE, which was then followed by a gradual decline in CPE representing the effect of mortality. For example, the large estimated year-class at Lake Guntersville in 2008 led to above-average CPE from 2008-2011, and the pattern was consistent for both the ADCNR and TVA electrofishing surveys. Age proportions of young fish (ages 1-3) were generally underestimated during years of large year-classes recruiting (Appendix A).

The sensitivity analysis indicated that estimates of R_t were robust to changes in assumptions about ESS, M, and σ_f (Figure 20). Mean percent change of R_t estimates were less than 1% under all ESS, M and σ_f scenarios. Temporal trends in F'_t were consistent across model scenarios; however, the magnitude of F'_t varied under different model scenarios (Figure 21). Instantaneous fishing mortality estimates decreased by an average of 6.88% as ESS increased to 60 and decreased by an average of 25.35% as ESS decrease to 20. Instantaneous fishing mortality estimates decreased by an average of 1.83% as σ_f decreased to 1.0e-10 F'_t and increased by an average of 3.83% as σ_f increased to 0.10. Instantaneous fishing mortality estimates increased by an average of 14.30% under the low M scenario and increased by an average of 14.0% under high M. Instantaneous fishing mortality rate also decreased by an average of 15.27% when M was allowed to decrease as a function of increased mean total length-at-age. Length at 50% vulnerability to sampling increased by an average of 47.65% when M was allowed to decrease as a function of increased mean total length-at-age. Survey vulnerability was not sensitive to changes in ESS or σ_f (Figure 22). Estimates of σ_s decreased when σ_f was increased and increased when ESS was increased. Estimates of σ_s were not sensitive to changes in assumptions about M. Including additional TVA CPE data did not change estimates of R_t, F'_t, and survey vulnerability, but resulted in lower estimates of σ_s. Model estimates of ADCNR CPE did not change drastically from the baseline model under the various scenarios (Figure 19).

The SCAA was able to estimate a time series of R_t and F'_t for all three impoundments, but not without a few problems. Parameter constraints during optimization were necessary for proper convergence of all three lake models, but maximum likelihood parameter estimates and confidence intervals were far removed from the bounds suggesting that the bounds improved optimization performance but did not influence the estimates. Under an ESS of 20 the Wheeler Reservoir model did not have a unisingular solution and thus did not converge. Also, standard error estimates were generally greater for lakes with lower sampling frequency. For example, R_t standard errors averaged 0.27 for Wheeler Reservoir, the lake with the lowest sampling frequency, 0.24 for Lake Guntersville and 0.19 for Demopolis Reservoir, the lake with the highest sampling frequency.

Discussion

Year-class strength is of major interest to fisheries scientists, managers, and anglers. Estimates of year-class strength from the SCAA model were robust to all changes in assumptions about M, ESS, and σ_f. These results suggest that the model may be useful for tracking and understanding variation in year-class strength, and may provide more reliable estimates than traditional catch curve residual methods. A simulation analysis by Tetzlaff (2011) concluded that SCAA could reliably estimate moderate fluctuations in year-class strength while catch curve methods could only detect extreme year-classes. I recommend that agencies adopt a method similar to this SCAA for estimating year-class strength through time, if the data are available.

Estimates of the magnitude of fishing mortality appear to be unrealistically high for these three stocks. Fishing mortality in a catch-and-release largemouth bass fishery is expected to be low and estimates of F'_t for similar largemouth bass stocks are variable from 0.07 at Sam Rayburn, Texas (Driscoll et al. 2007) and 0.12 at Rodman Reservoir, Florida (Henry 2003) to 0.584 at a Puerto Rico reservoir (Waters et al. 2005). Average estimates of F'_t from Demopolis and Wheeler reservoirs were 0.66 and 0.63 respectively, which is much higher than published estimates from other similar systems. The inflated estimate of F'_t may be related to assumptions regarding vulnerability to fishing as well as survey vulnerability (Punt et al. 2014). The model assumed a sigmoidal vulnerability schedule in which vulnerability approaches an asymptote of 1.0. If the true shape of these vulnerability schedules is not sigmoidal but instead dome shaped (Bayley and Austen 2002) and vulnerability decreases past some threshold total length, then the only way for the model to account for the rate of decay in the age proportion data is by increasing the estimate of F'_t. Independent estimates of F'_t obtained through tagging studies (Miranda and Dorr 2000; Newby et al. 2000) could inform the model about F'_t directly, thereby providing indirect information on M and potentially allowing the model to estimate the shape of the vulnerability functions.

Understanding fishing or survey vulnerability can allow the size distribution of a population to be inferred from fisheries or survey catch (Millar 1992). Assumptions about vulnerability such as the shape of the curve is a critical consideration in stock assessment (Millar 1992; Maunder and Harley 2011) and can have significant influences on estimates. Punt et al. (2014) demonstrated the influence of different assumptions about natural mortality, vulnerability, and recruitment can have on F'_t. Allowing for natural mortality trends with age, vulnerability trends with age, and recruitment trends with time, despite resulting in identical catch-at-age predictions, estimated markedly different estimates of F, 0.2 yr^{-1}, 0.29 yr^{-1}, and 0.15 yr^{-1} respectively. I assumed a sigmoidal or asymptotic length based fishing and survey vulnerability schedule, which is common in stock assessments (Smith and Punt 1998; Helu et al. 2000). Dome shaped schedules have been used (Millar 1992; Thompson 1994; Helu et al. 2000) and have been estimated indirectly for gillnets and boat electrofishing (Hansen et al. 1997; Bayley and Austen 2002). Another approach is to estimate individual age specific parameters with no assumed functional form, but are constrained on how much vulnerability can vary from age to age using a smoothness penalty to avoid over parameterization of the model (Haist et al. 1999; Ianelli 2002; Maunder and Watters 2003). A knife edge fishing vulnerability schedule, which assumes no fishing vulnerability below a minimum length limit, has a maximum vulnerability at the minimum length limit, and then declines exponentially with length, has been assumed (Tetzlaff et al. 2011). Fishing vulnerability has been estimated using tag returns to obtain age or size specific catch data from the fishery (Miranda and Dorr 2000; Newby et al. 2000) and this information could aid in the estimation of fishing vulnerability within this model. A mark recapture study could provide similar information about survey vulnerability (Buckmeier and Schlechte 2011). The influences of different assumptions about vulnerability on parameter estimates could be significant and must be considered (Maunder and Harley 2011).

Inaccuracies in the assumed partitioning between F'_t and M may have also resulted in inflated F'_t estimates. For example, the assumed constant M, estimated from Jensen (1996), Hoenig (1983), and Pauly (1980) (Table 10), were low compared with estimates of 0.39 from Sam Rayburn, Texas (Driscoll et al. 2007), 0.54 from Rodman Reservoir, Florida (Henry 2003), and 0.46 from a summary of 698 largemouth bass populations (Beamesderfer and North 1995). Another possibility is that the model did not account for catch and release mortality. Largemouth bass post-release mortality rates have been estimated to be 30.8% (9.1-68.4%; Weathers and Newman 1997) at Lake Eufaula, Alabama, 26.7% (5.2-47.8% Schramm et al. 1987) at Orange and Lochloosa Lakes, Florida, and 28.3% for 44 tournaments throughout the eastern United States (Wilde 1998). Catch and release mortality could account for a significant portion of total mortality that was not described within the model. Catch and release mortality would increase the decay rate in proportion at age of ages where vulnerability to fishing is low given the assumed MLL and survey vulnerability is high. The only way for the model to account for this is by estimating a high F'_t. This theory is support by the fact that the lowest estimates of F'_t occur in the size-specific M model that allows higher M on smaller fish. The cause of unrealistically high F'_t estimates must be established before this SCAA approach can be a reliable tool for estimating fishing mortality rates in freshwater recreational fisheries such as largemouth bass.

The effective sample size for age composition data (ESS) is often a controversial topic in stock assessments and can have significant influences on parameter estimates. In my analysis I assumed a range of ESS values (20, 40, 60) to first assess how sensitive the parameter estimates were to changes in ESS in the context of a typical largemouth bass stock data set. My sensitivity analysis demonstrated that data weighting had little influence on year-class strength estimates within the framework of this SCAA; however, F'_t was sensitive to changes in ESS. My approach was valid, but other approaches have also been used. Francis (2011) suggested that for data weighting in statistical fisheries stock assessment models, abundance data should not be down weighted because it is thought they may be unrepresentative or in order to fit other data. One such approach is to estimate ESS within the model (Maunder 2011; Francis 2011) via an iterative re-weighting procedure or modeling the age/length proportion correlations themselves (Miller and Skalski 2006). Deriso et al. (1985) found that a similar model for Pacific halibut was robust to moderate changes to weighting factors; however, this is not always the case (Crone and Sampson 1998). Sensitivity of model estimates to changes in ESS may be stock specific and should be evaluated for individual stocks. If estimates are sensitive to changes in ESS, then it may be beneficial to estimate ESS within the model via a number of methods (Maunder 2011).

The Wheeler Reservoir SCAA failed to converge at under a low assumed ESS (20). It is possible that given a combination of assigning higher weight to CPE data and too few CPE data to inform the model, there was no singular combination of parameter estimates that maximized the objective function. Wheeler Reservoir had data on 44% of years included with the largest gap between year with data of 4 years. This could be an indication of the SCAA approaching its missing data limitations; however, my study was not designed to determine the minimum data requirements for this type of SCAA. Future work should explore model performance via simulation-estimation trails whereby analysis iteratively fits the model to simulated data sets that challenge the model assumptions.

One of the strengths of the SCAA approach is that it has the flexibility to incorporate many forms of supplemental data. Fishery independent data inputs such as standardized samples and mark recapture studies, and fishery dependent data such as creel surveys and tagging studies can be included in the model to improve model fit and certainty. Supplemental data can support or contradict existing data, and can be helpful in deciding whether extremes in CPE data are representative of the stock. I explored the addition of TVA electrofishing survey CPE data and found that model estimates did not greatly differ from the baseline model. The similarity in model estimates suggested some degree of consistency in CPE trends between TVA and ADCNR surveys. Maunder and Punt (2013) provide a thorough review of integrated analysis in fisheries stock assessments where examples of length-frequency data, growth estimation, age composition, CPE data, stock-recruitment analysis, and tagging data have all been used to create an integrated analysis to improve model performance and certainty. Although few freshwater recreational fisheries have all of these data types available, undoubtedly future stock assessment work on important recreational species such as largemouth bass could place more emphasis on using available data types in a more holistic modeling approach such as the SCAA.

IV. Conclusion

In an effort to understand the possible causes of the observed difference in size structure between Guntersville and Wheeler reservoirs two approaches were taken. To investigate if variation in growth or mortality could explain the difference in size structure I compared a number of population characteristics, assessed an association between early growth and natural mortality, and explored the individual largemouth bass probability of reaching 500 mm using a simple per recruit model. To examine whether recent recruitment trends could explain the difference in size structure I fit a SCAA model to reconstruct recruitment and fishing mortality time series’ using age composition and relative abundance data.

Differences in growth alone could not explain the observed variation in size structure. Recent recruitment trends estimated from the SCAA also do not diverge enough between lakes to explain the difference in size structure. The results of this study suggested that variation in mortality is likely the cause for the variation in size structure and that differences in early growth can explain the variation in natural mortality of largemouth bass in Wheeler and Guntersville reservoirs. This difference in early growth is likely due to a difference in diet that may be dictated by habitat difference such as macrophyte coverage. This study reiterates the interrelated nature of life history parameters growth, mortality and age-at-maturity where reproductive fitness is optimized by adjusting age-at-maturity given a trade-off between growth and mortality.

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Table 1.

Year	Sex	Model	Parameters	AICc	ΔAIC	Weight
2013	Female	Null	3	195.82	0.00	0.37
		t0	4	197.06	1.24	0.20
		k	4	198.39	2.57	0.10
		L∞,k	5	198.54	2.72	0.10
		L∞,t0	5	198.86	3.04	0.08
		L∞	4	198.88	3.06	0.08
		k,t0	5	199.69	3.87	0.05
		Full	6	202.44	6.62	0.01
2013	Male	k	4	151.62	0.00	0.47
		L∞,k	5	153.39	1.76	0.19
		Full	6	154.74	3.12	0.10
		k,t0	5	155.05	3.43	0.08
		t0	4	155.15	3.52	0.08
		Null	3	156.46	4.83	0.04
		L∞	4	158.33	6.71	0.02
		L∞,t0	5	158.83	7.21	0.01
2014	Female	Null	3	188.91	0.00	0.27
		k	4	189.01	0.09	0.26
		L∞	4	189.45	0.54	0.21
		t0	4	190.61	1.70	0.12
		k,t0	5	192.32	3.41	0.05
		L∞,k	5	192.46	3.54	0.05
		L∞,t0	5	192.80	3.88	0.04
		Full	6	196.32	7.41	0.01
2014	Male	Null	3	152.32	0.00	0.26
		Full	6	152.36	0.03	0.26
		k	4	152.86	0.54	0.20
		L∞	4	154.48	2.16	0.09
		k,t0	5	154.62	2.29	0.08
		t0	4	155.20	2.88	0.06
		L∞,k	5	156.26	3.94	0.04
		L∞,t0	5	158.40	6.07	0.01

Table 2.

Year	Sex	Lake	L∞	k	to
2013	Female	Guntersville	552.66	0.30	-0.41
		Wheeler	546.79	0.31	-0.52
	Male	Guntersville	452.63	0.49	-0.06
		Wheeler	449.03	0.57	-0.04
2014	Female	Guntersville	529.60	0.33	-0.07
		Wheeler	533.54	0.34	-0.09
	Male	Guntersville	484.49	0.35	-0.24
		Wheeler	474.54	0.42	-0.05

Table 3.

M Scenario	Model	Parameters	AICc	ΔAIC	Weight
Baseline (Med)	Growth	17	243.75	0.00	0.34
	Sex.Growth	18	243.77	0.02	0.34
	Lake.Growth	18	246.71	2.96	0.08
	Full	19	246.80	3.05	0.07
	Null	16	246.94	3.19	0.07
	Sex	17	247.21	3.46	0.06
	Lake	17	249.64	5.89	0.02
	Separate F	17	249.70	5.95	0.02
	Lake.Sex	18	250.09	6.34	0.01
Hoenig (High)	Sex.Growth	18	243.48	0.00	0.49
	Growth	17	244.80	1.32	0.25
	Full	19	246.37	2.89	0.12
	Lake.Growth	18	247.71	4.23	0.06
	Sex	17	248.12	4.65	0.05
	Null	16	250.05	6.57	0.02
	Lake.Sex	18	250.84	7.36	0.01
	Lake	17	252.89	9.41	0.00
Pauly (Low)	Growth	17	243.86	0.00	0.38
	Sex.Growth	18	244.78	0.93	0.24
	Null	16	246.24	2.38	0.12
	Lake.Growth	18	246.67	2.81	0.09
	Sex	17	247.32	3.47	0.07
	Full	19	247.54	3.68	0.06
	Lake	17	249.13	5.27	0.03
	Lake.Sex	18	250.26	6.40	0.02

Table 4.

Guntersville			Wheeler		
	Female	Male		Female	Male
Fast	0.143	0.145	Fast	0.195	0.244
Med	0.140	0.184	Med	0.210	0.144
Slow	0.182	0.206	Slow	0.101	0.106

Table 5.

Parameter	Pauly (Low)	Basline (Med)	Hoenig (High)
F	0.214	0.101	0.006
h	0.023	0.023	0.024
L50	250	261	272
σ	0.660	0.656	0.653
C	0.901	0.730	0.673
Male	-0.026	-0.040	-0.063
Wheeler	-0.004	0.001	0.004

Table 6.

Analysis	Model	Parameters	AICc	DeltaAIC	Weight
Length-at-Maturity	Null	1	252.6	0	0.44
	Interaction	3	253.01	0.41	0.35
	Additive	2	254.05	1.45	0.21
Age-at-Maturity	Interaction	3	278.36	0	0.74
	Additive	2	281.66	3.29	0.14
	Null	1	282.04	3.67	0.12

Table 7.

M Scenario	Analysis	φ Ratio	Δφ	Rank
Baseline	Baseline	0.9154	0	
	M	0.9172	0.0020	1
	F	0.9155	0.0001	2
	MLL	0.9154	0.0000	3
M = 0.1	Baseline	1.0053	0	
	M	1.0066	0.0013	1
	F	1.0054	0.0002	2
	MLL	1.0053	0.0000	3
M = 0.5	Baseline	0.8866	0	
	M	0.8887	0.0022	1
	F	0.8867	0.0001	2
	MLL	0.8866	0.0000	3
Baseline	Baseline	0.9154	0	
	ΔM	1.1017	0.1864	1
	MLL	0.9168	0.0015	4
	Twice F	0.9278	0.0124	3
	Wheeler F > Guntersville F	0.9620	0.0467	2

Table 8.
Symbols and descriptions of variables used for statistical catch at age model

Symbol	Description	Value (if needed)
$\boldsymbol{R_0}$	Average recruitment	1
$\boldsymbol{R_t}$	Annual recruitment	
$\boldsymbol{N_{t,a}}$	Abundance at time and age	
$\boldsymbol{Z_{t,a}}$	Total instantaneous mortality rate at time and age	
$\boldsymbol{F_{t,a}}$	Instantaneous fishing mortality rate at time and age	
$\boldsymbol{M}$	Instantaneous natural mortality	Average of Pauly (1980), Hoenig (1983), and Jensen (1996)
$\boldsymbol{S_{a,f}}$	Fishery size-based, age-specific vulnerability	
$\boldsymbol{S_{a,s}}$	Sampling size-based, age-specific vulnerability	
$\boldsymbol{h}$	Steepness parameter for survey vulnerability function	
$\boldsymbol{L_{50}}$	Length at 50% survey vulnerability	
$\boldsymbol{tl_a}$	Mean length-at-age	$tl_a = Linf\left(1 - e^{-k(age-t0)}\right)$
$\boldsymbol{E_t}$	Observed survey effort	
$\boldsymbol{q}$	ADCNR survey catchability	
$\boldsymbol{q_{tva}}$	TVA survey catchability	
$\boldsymbol{I_{t,a}}$	Survey catch at time and age	
$\boldsymbol{\tilde{I}_t}$	Observed survey catch per effort	
$\boldsymbol{I_t}$	Survey catch per effort	
$\boldsymbol{\hat{u}_{t,a}}$	Observed proportion of catch-at-age in survey	
$\boldsymbol{u_{t,a}}$	Proportion of catch-at-age in survey	
$\boldsymbol{\widetilde{tva}_t}$	Observed TVA survey catch per effort	
$\boldsymbol{tva_t}$	Survey TVA catch per effort	
$\boldsymbol{\omega_t}$	Deviations for random walk: fishing mortality	
$\boldsymbol{\sigma_f}$	Standard deviations for $\log_e$ random walk	0.05
$\boldsymbol{\sigma_r}$	Standard deviations for $\log_e$ of recruitment variation	0.05
$\boldsymbol{\sigma_s}$	Standard deviations for $\log_e$ of survey catch per effort error	
$\boldsymbol{M_a}$	Size-based, age-specific instantaneous natural mortality	

Table 9.
Population generating equations

Population model equations		Description
$N_{t+1,a+1} = N_{t,a}e^{-Z_{t,a}}$	(T9.1)	Abundance at time and age
$R_1 = e^{-\sum_t \log_e R_t}$	(T9.2)	Initial recruitment in year one
$Z_{t,a} = M + F_{t,a}$	(T9.3)	Total instantaneous mortality
$F_{t,a} = f_t S_{a,f}$	(T9.4)	Instantaneous fishing mortality
$\log_e f_{t+1} = \log_e f_t + \omega_t; \omega_t \sim N(0, \sigma_f^2)$	(T9.5)	Fishing mortality random walk process
$I_{t,a} = N_{t,a}E_t S_{a,s} q$	(T9.6)	Survey catch at time and age
$S_{a,s} = 1/(1 + e^{-h(tl_a - L_{50})})$	(T9.7)	Survey vulnerability at age
$I_t = \sum_a I_{t,a} / E_t$	(T9.8)	Survey catch per effort
$u_{t,a} = \frac{I_{t,a}}{\sum_a I_{t,a}}$	(T9.9)	Proportion at age in survey catch
$M_a = M \frac{(0.66 * linf)}{tl_a}$	(T9.10)	Age specific, size-based natural mortality

Table 10.
Objective function equations for statistical catch at age model

$L = \sum_i l_i$	(T10.1)	Objective function
$l_1 = \log_e(I_t) \sim Norm(\tilde{I}, \sigma_s)$	(T10.2)	Survey catch-per-effort
$l_2 = \log_e\left(u_{t,a}\right) \sim Multinom(\tilde{u}_{t,a}, ESS)$	(T10.3)	Proportion at age in survey catch
$l_3 = \log_e(R_t) \sim Norm(0, \sigma_r)$	(T10.4)	Recruitment
$l_4 = \log_e(\omega_t) \sim Norm(0, \sigma_f)$	(T10.5)	Random walk fishing mortality
$l_5 = 1000\left(S_{14,s} - 1\right)^2$	(T10.6)	Survey vulnerability penalty
$l_6 = \log_e(tva_t) \sim Norm(\widetilde{tva}_t, \sigma_s)$	(T10.7)	TVA catch-per-effort

Table 11.
Scenario assumptions for sensitivity analysis

Variable	Level	Value
M	Low	0.26[pd], 0.24[pg], 0.26[pw]
	* Medium	0.31[ad],0.29[ag], 0.32[aw]
	High	0.35[hd], 0.33[jg], 0.35[hw]
ESS	Low	20
	* Medium	40
	High	60
σ_f	Low	1.0e-10
	* Medium	0.05
	High	0.1
TVA	* Out	
	In	
M_a	* Out	
	In	

* denotes baseline model conditions

[p] Pauly (1980)

[h] Hoenig (1983)

[j] Jensen (1996)

[a] Average

[d] Demopolis Reservoir

[g] Lake Guntersville

[w] Wheeler Reservoir

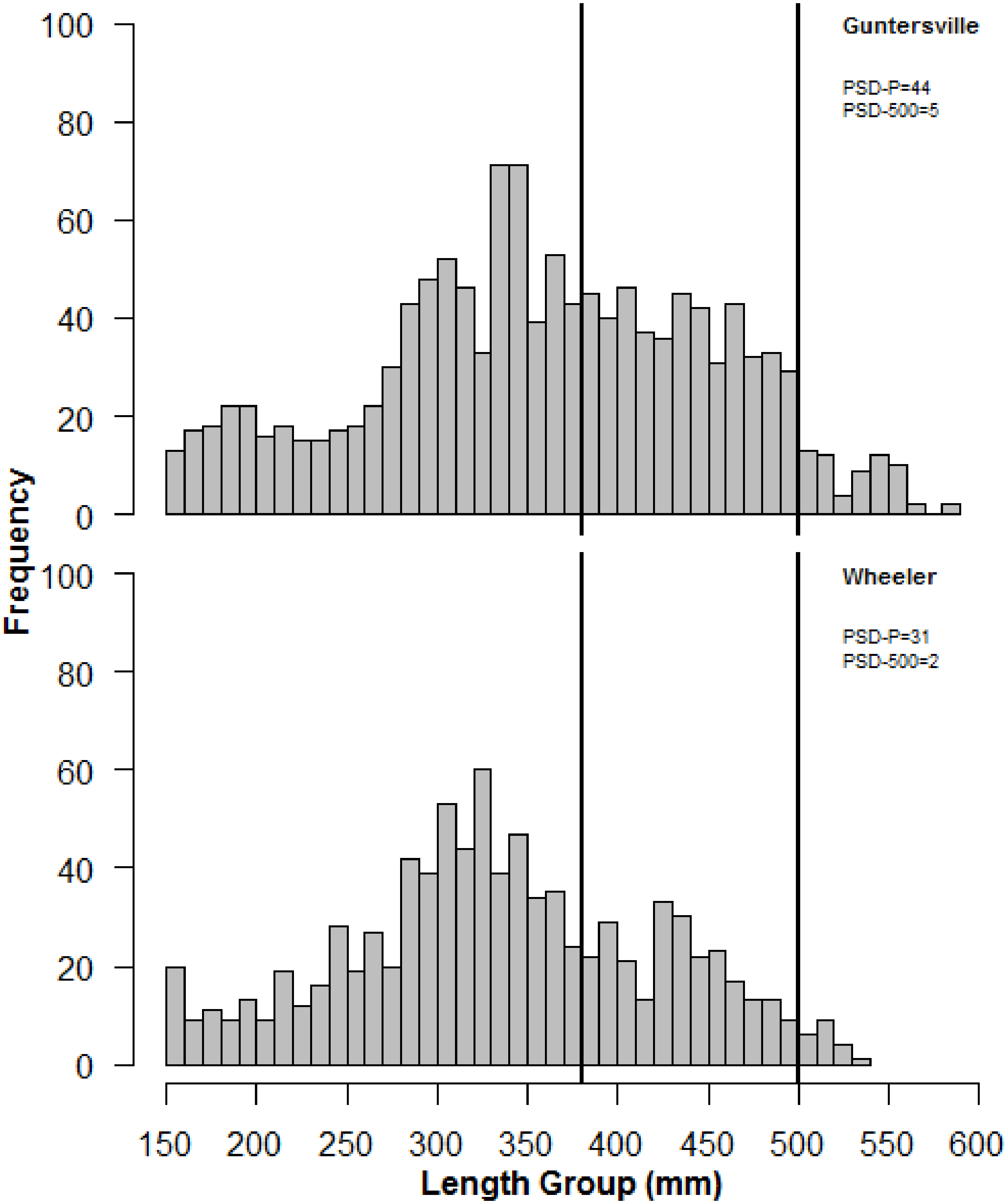
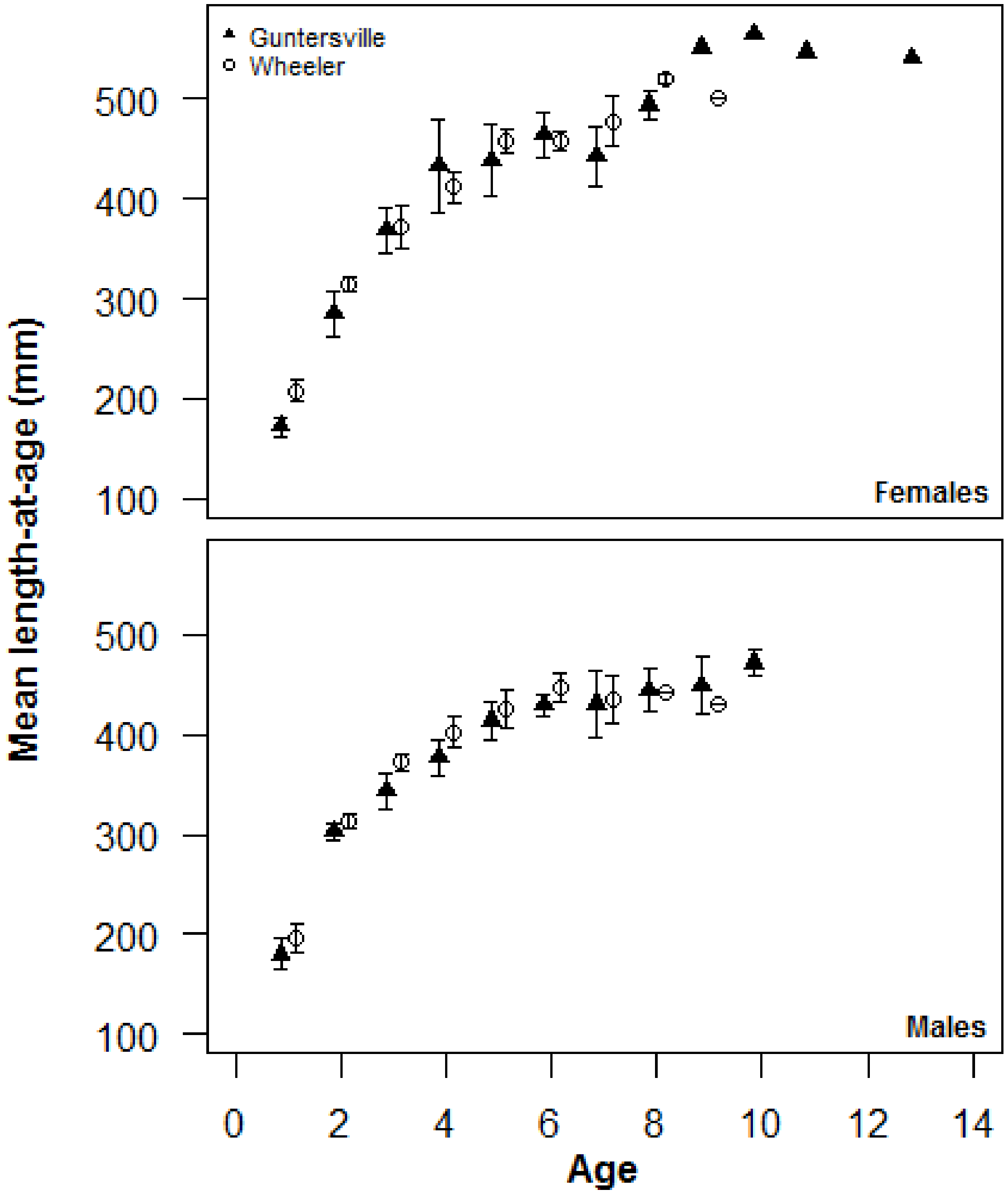

Guntersville
PSD-P=44
PSD-500=5
Wheeler
PSD-P=31
PSD-500=2
Frequency
0
20
40
60
80
100
150
200
250
300
350
400
450
500
550
600
Length Group (mm)

Figure 1.



▲ Guntersville
○ Wheeler
Females
Males
Mean length-at-age (mm)
100
200
300
400
500
100
200
300
400
500
0
2
4
6
8
10
12
14
Age

Figure 2.

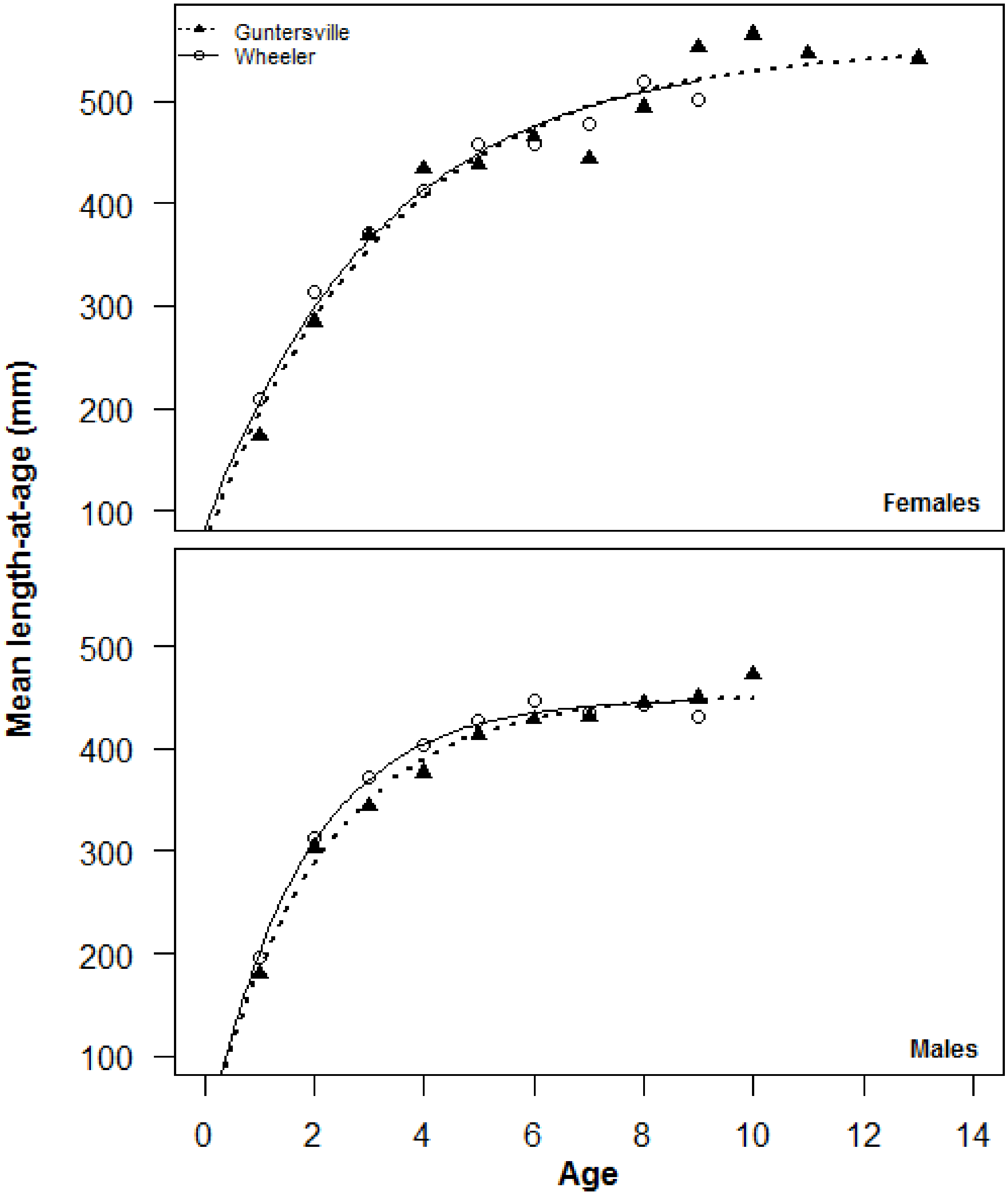
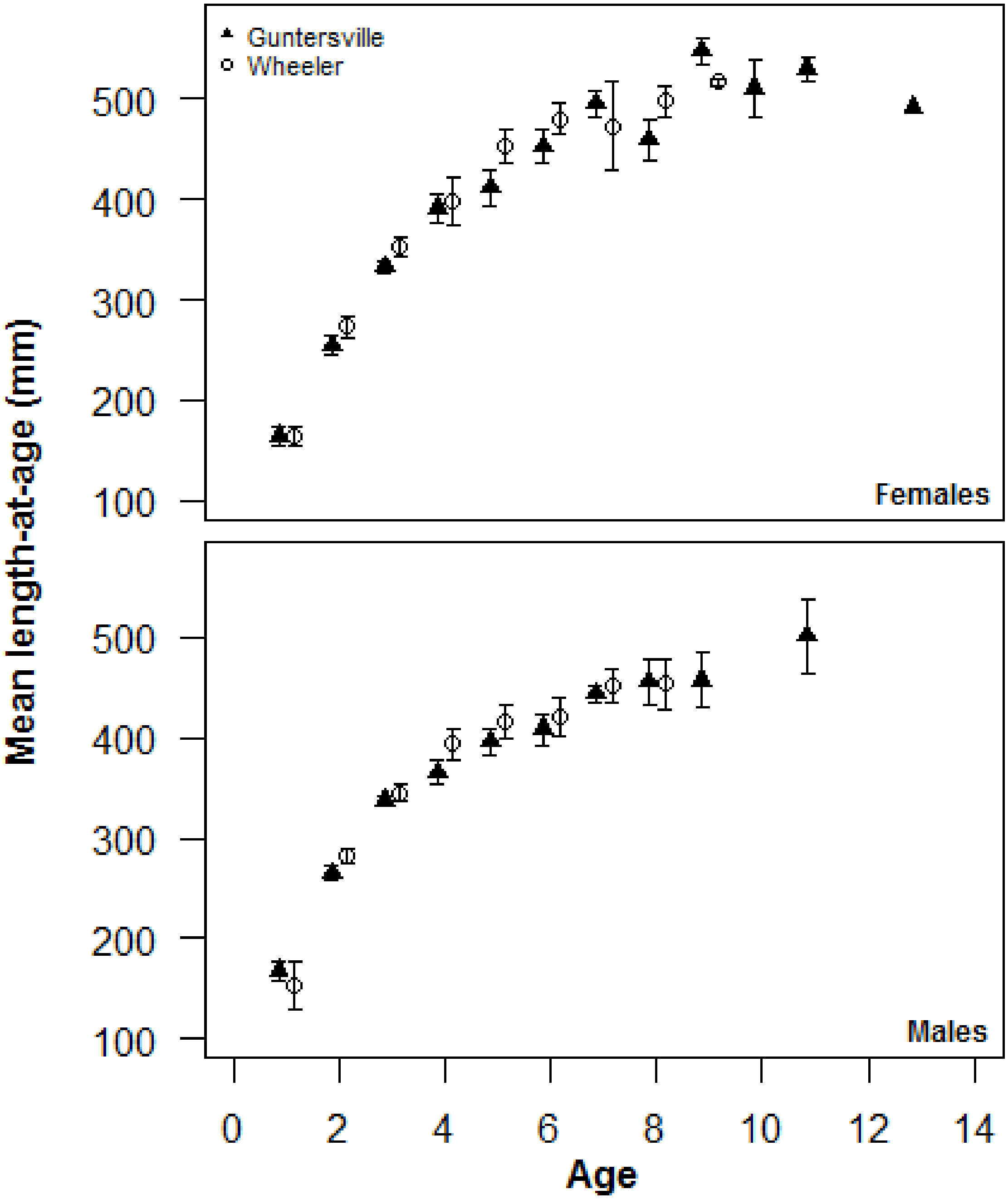

Guntersville
Wheeler
Mean length-at-age (mm)
100
200
300
400
500
Females
Males
0
2
4
6
8
10
12
14
Age

Figure 3.



▲ Guntersville
○ Wheeler
Females
Males
Mean length-at-age (mm)
100
200
300
400
500
0
2
4
6
8
10
12
14
Age

Figure 4.

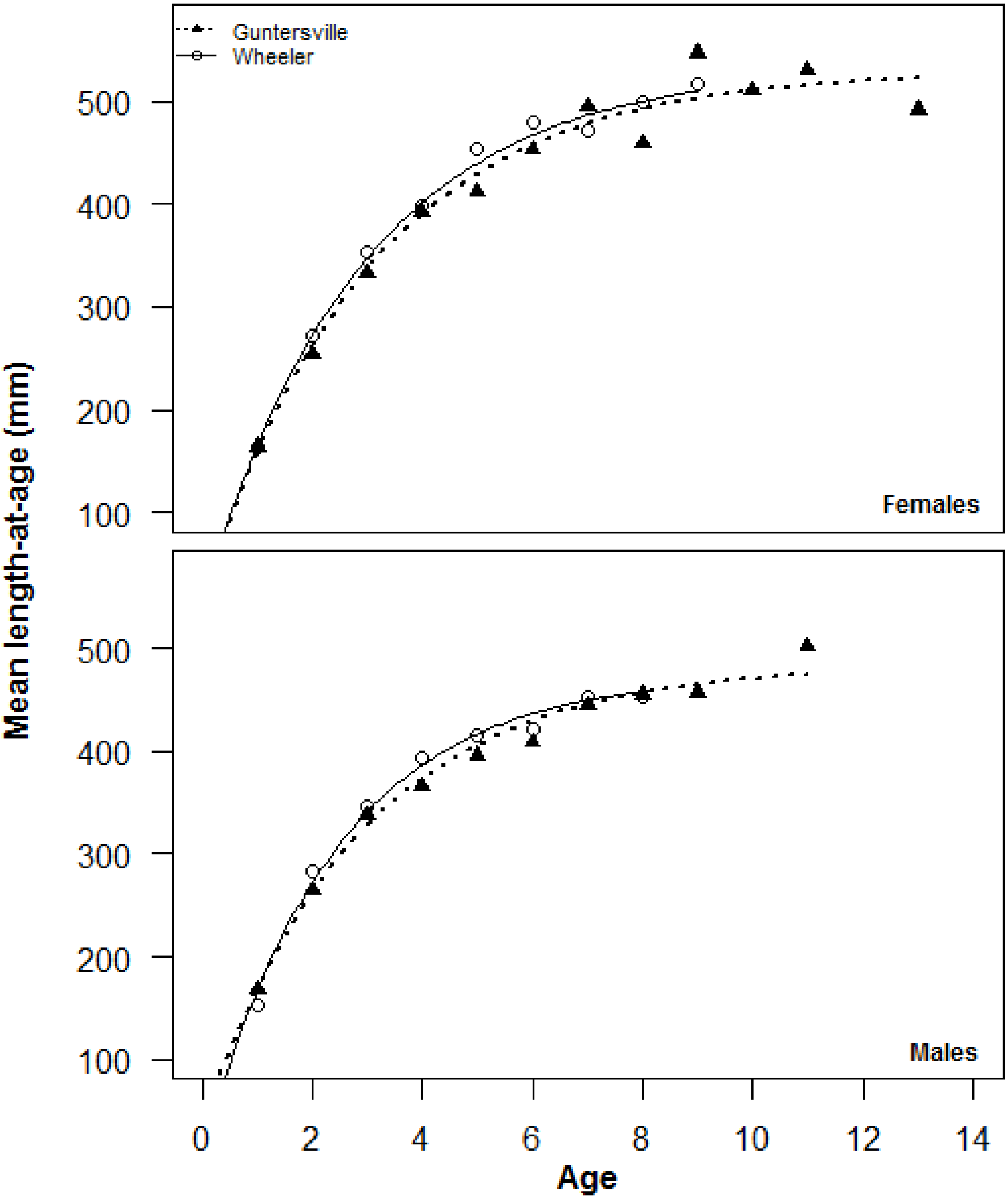

Guntersville
Wheeler
500
400
300
200
100
Females
500
400
300
200
100
Males
Mean length-at-age (mm)
0
2
4
6
8
10
12
14
Age

Figure 5.

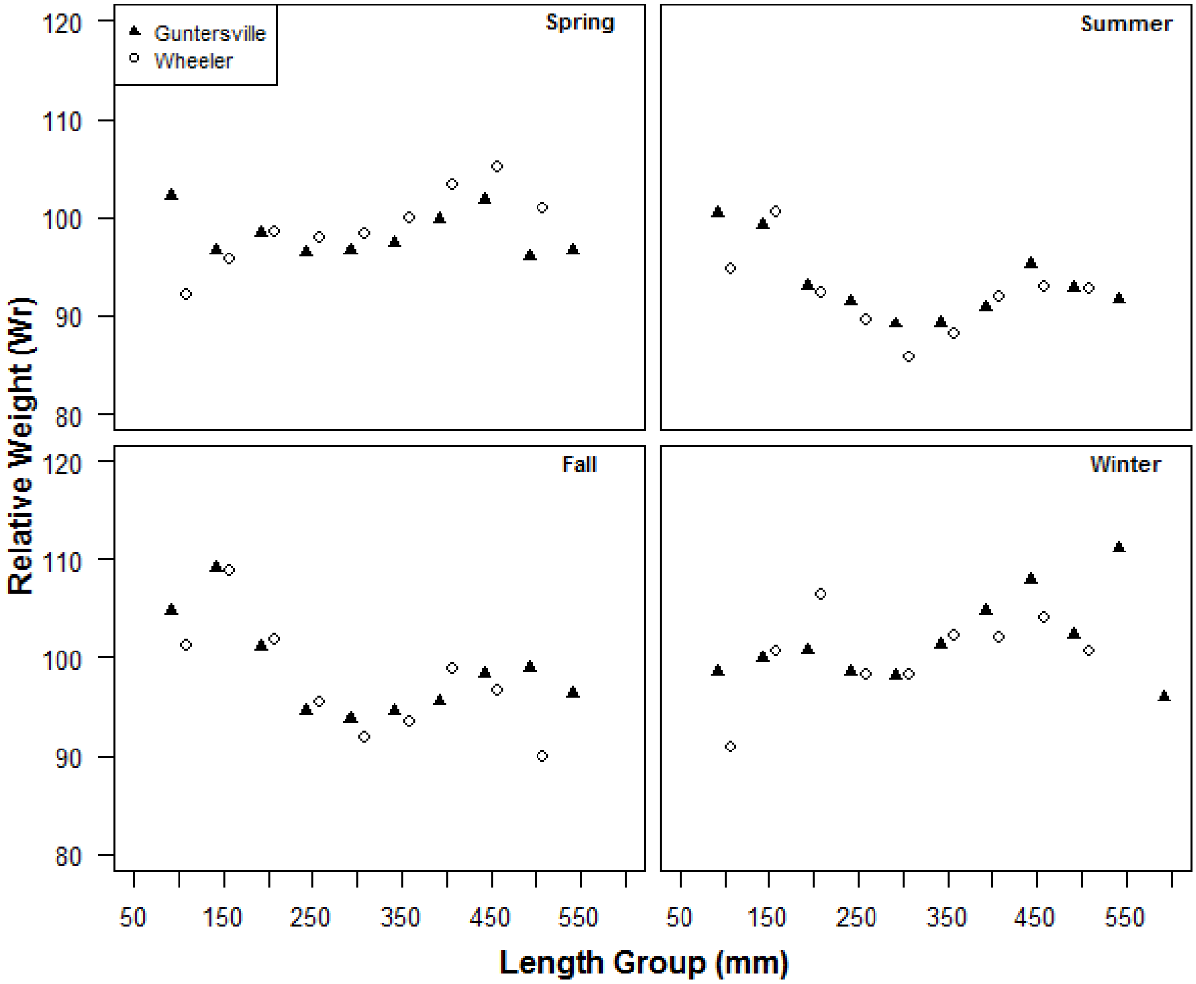

Guntersville
Wheeler
Spring
Summer
Fall
Winter
Relative Weight (Wr)
120
110
100
90
80
50
150
250
350
450
550
Length Group (mm)

Figure 6.

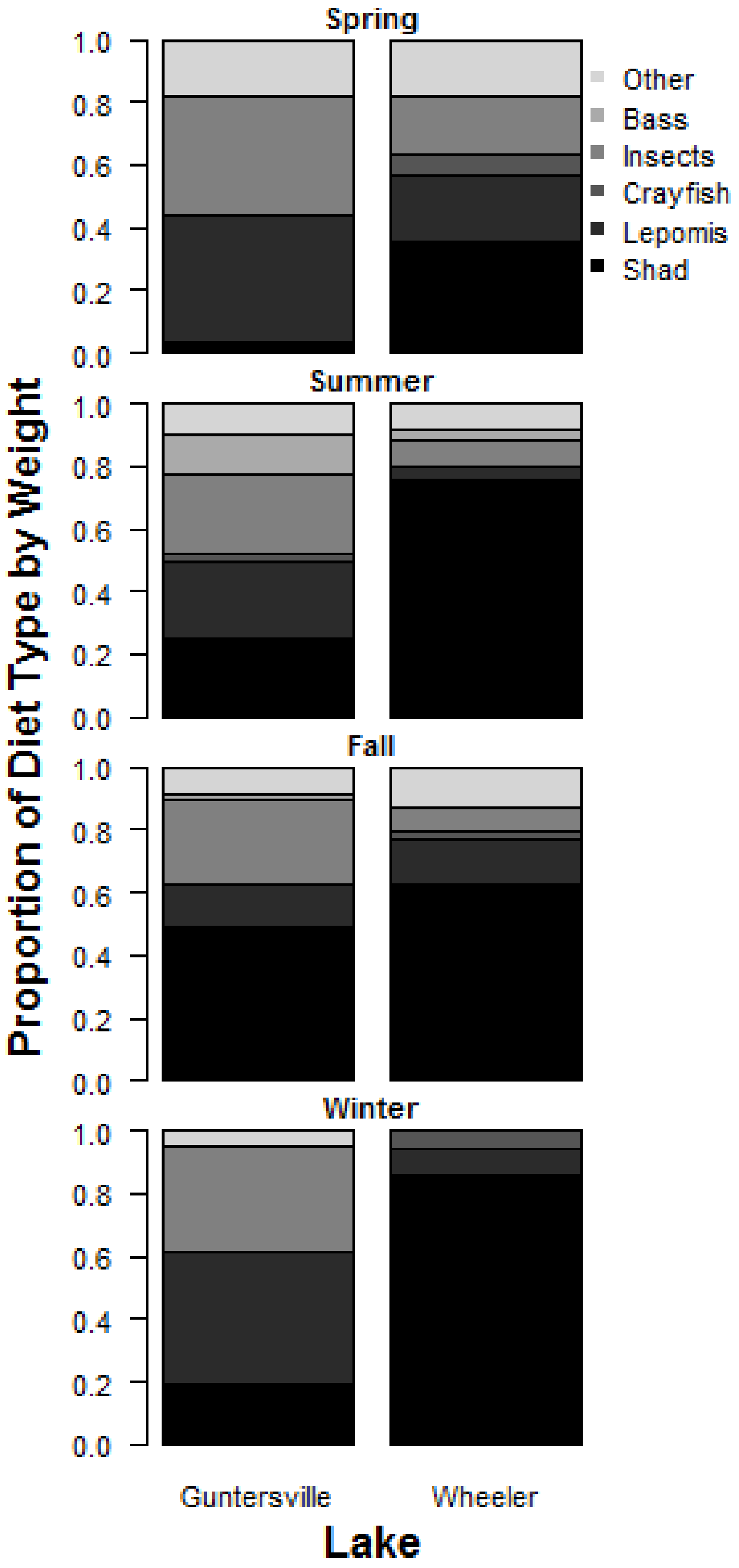
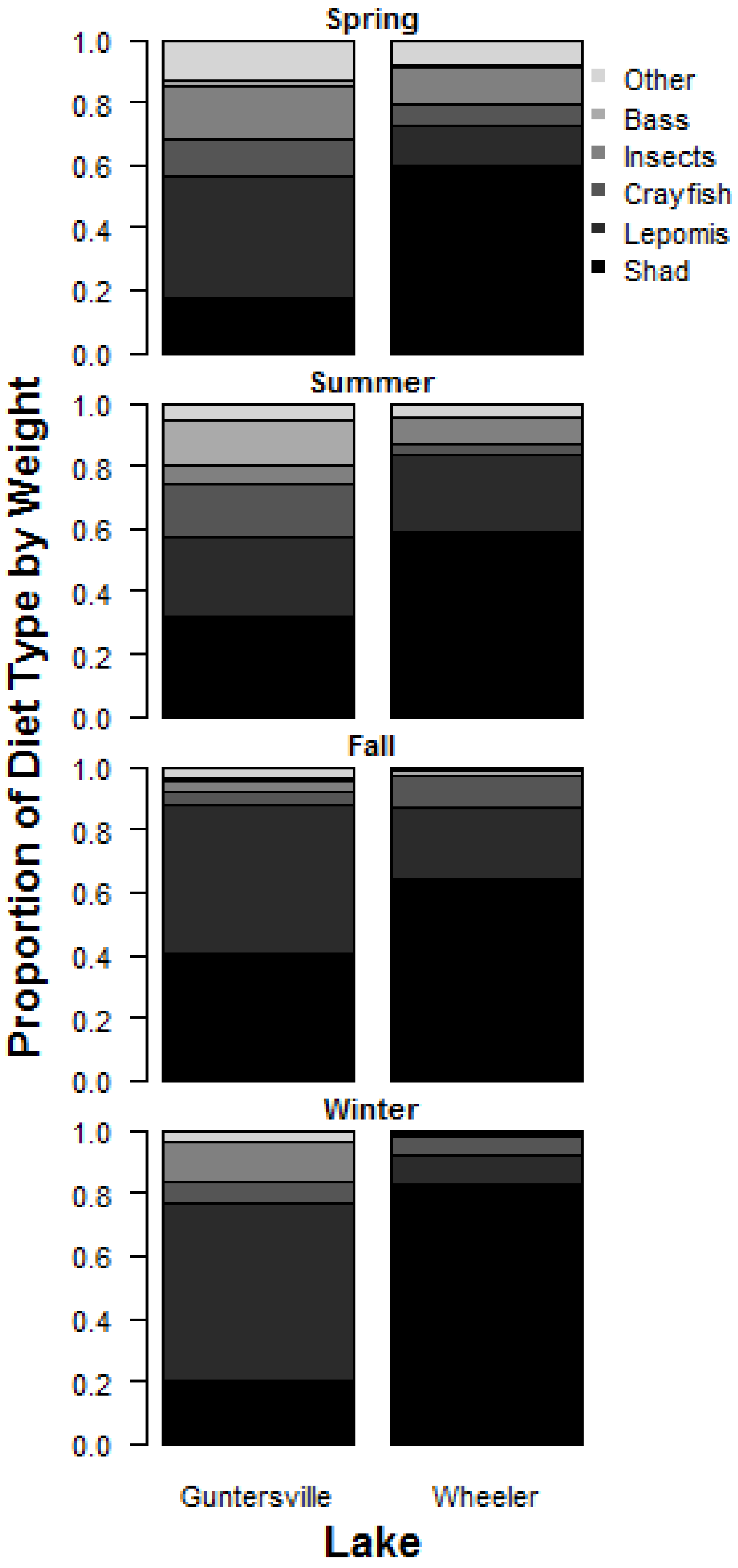

Spring
Summer
Fall
Winter
Other
Bass
Insects
Crayfish
Lepomis
Shad
1.0
0.8
0.6
0.4
0.2
0.0
Proportion of Diet Type by Weight
Guntersville
Wheeler
Lake

Figure 7.


Spring
Summer
Fall
Winter
1.0
0.8
0.6
0.4
0.2
0.0
Other
Bass
Insects
Crayfish
Lepomis
Shad
Proportion of Diet Type by Weight
Guntersville
Wheeler
Lake

.

Figure 8.

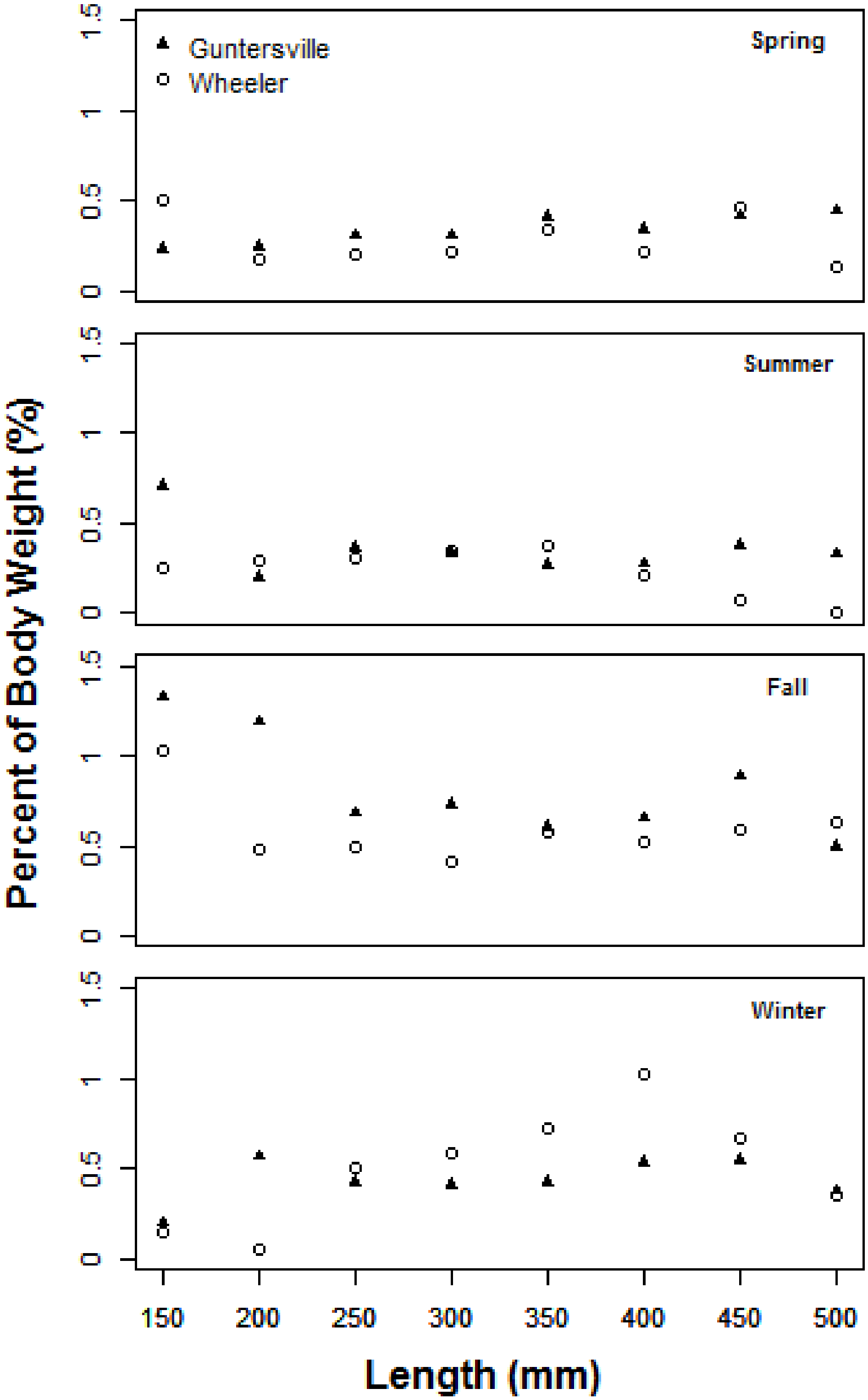

Guntersville
Wheeler
Spring
Summer
Fall
Winter
Percent of Body Weight (%)
0
0.5
1
1.5
150
200
250
300
350
400
450
500
Length (mm)

Figure 9.

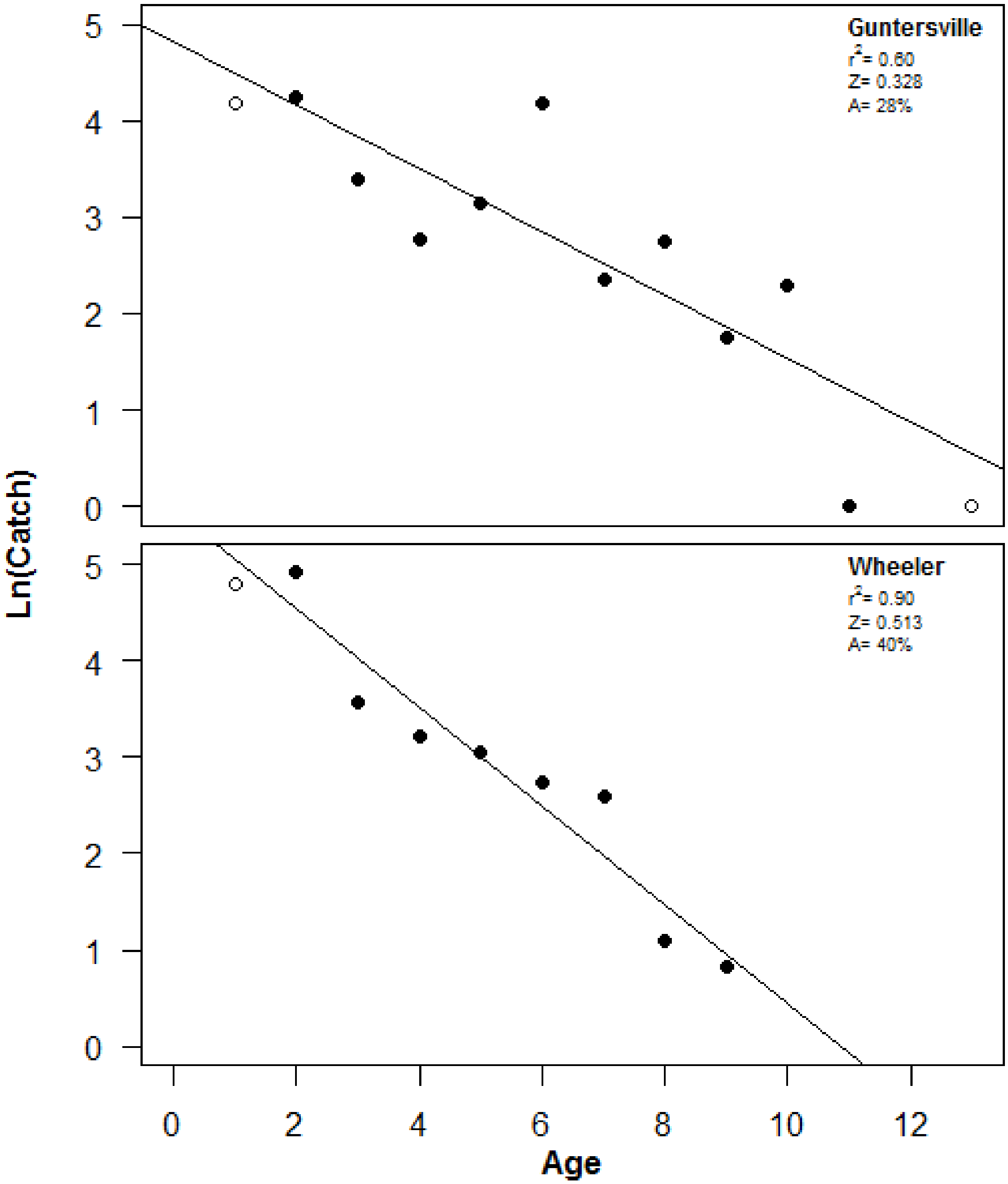

Guntersville
r^2= 0.60
Z= 0.328
A= 28%
Wheeler
r^2= 0.90
Z= 0.513
A= 40%
Ln(Catch)
Age
0
1
2
3
4
5
0
2
4
6
8
10
12

Figure 10.

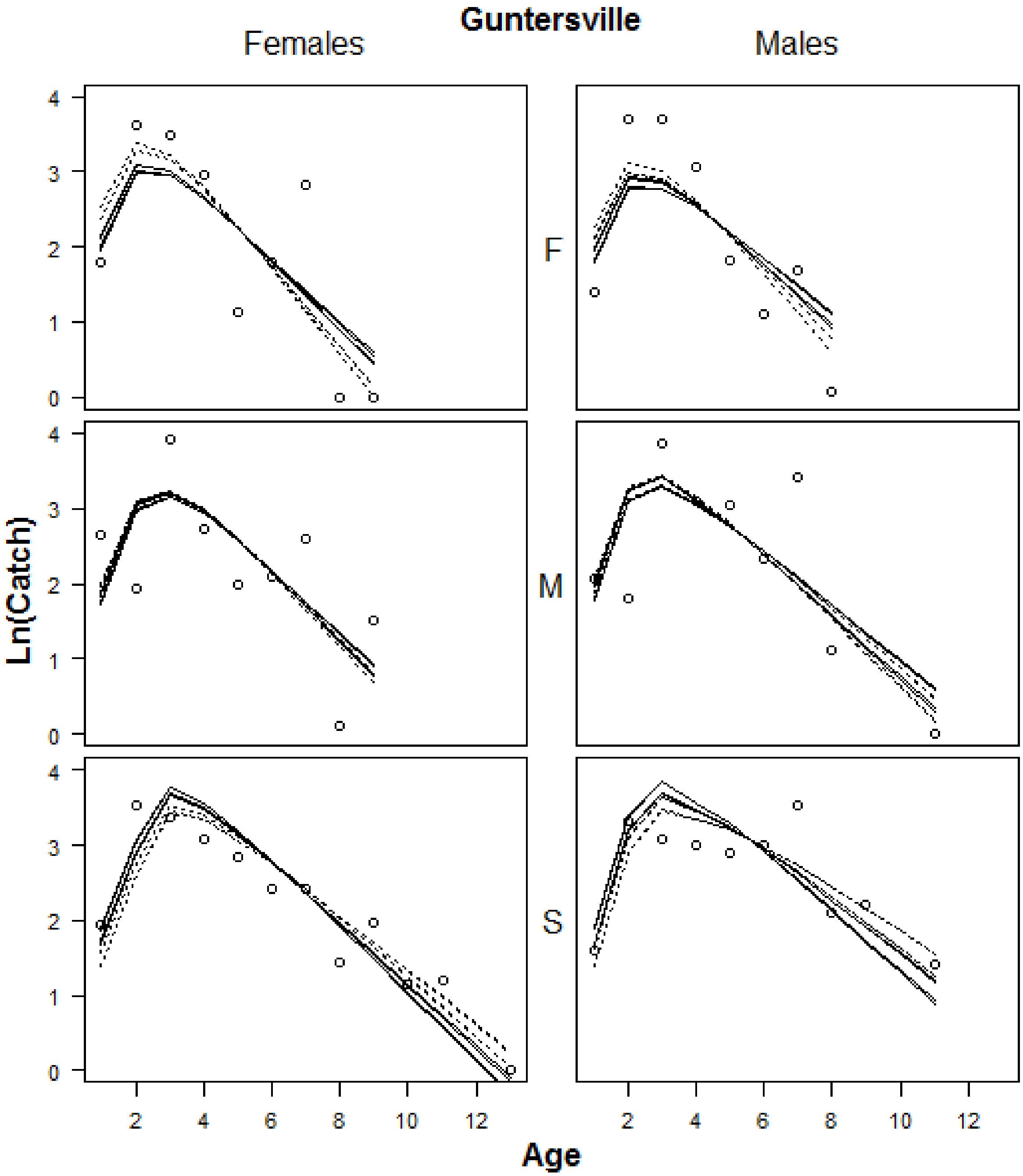

Guntersville
Females
Males
F
M
S
Ln(Catch)
Age
0
1
2
3
4
2
4
6
8
10
12

Figure 11.

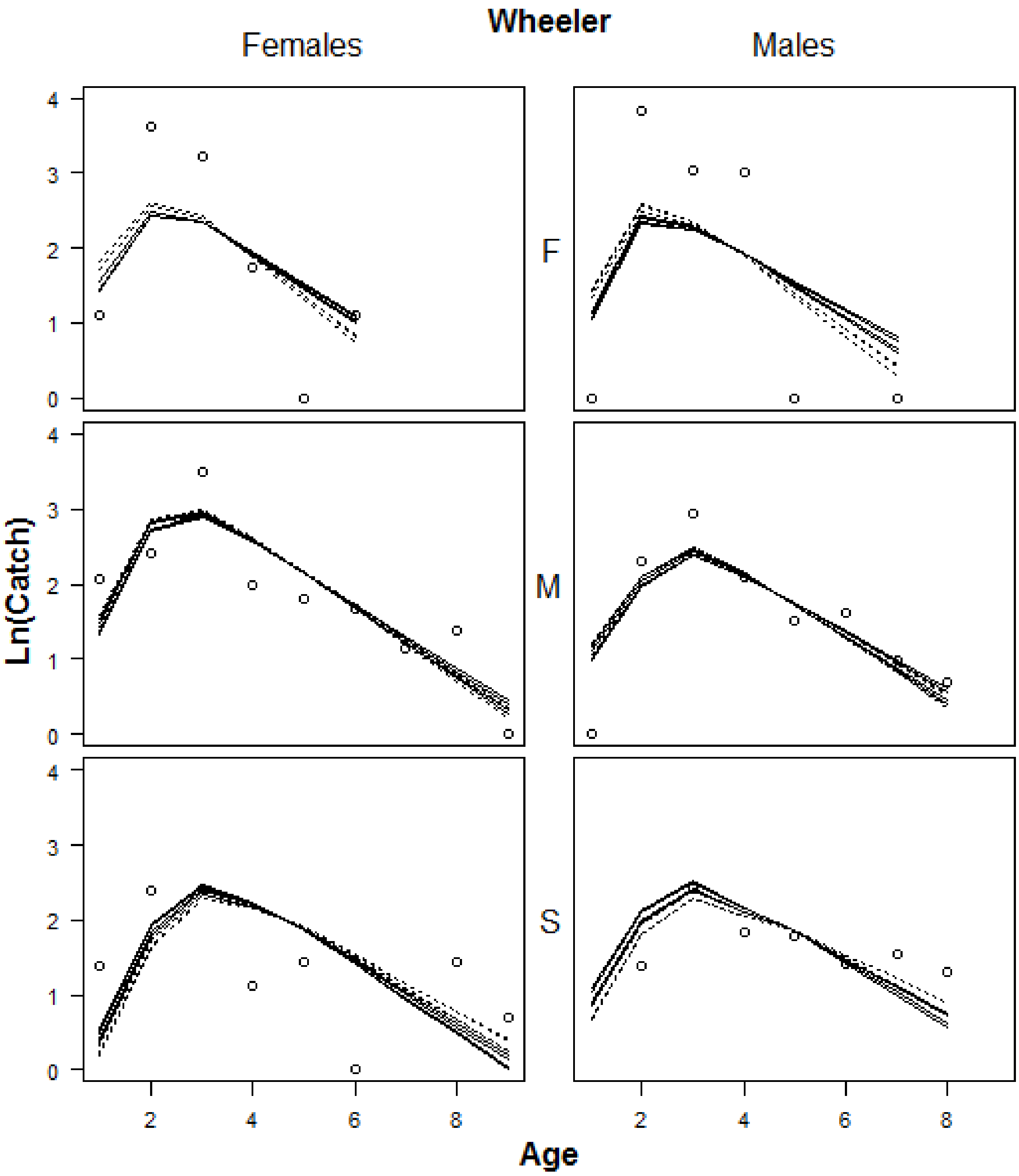
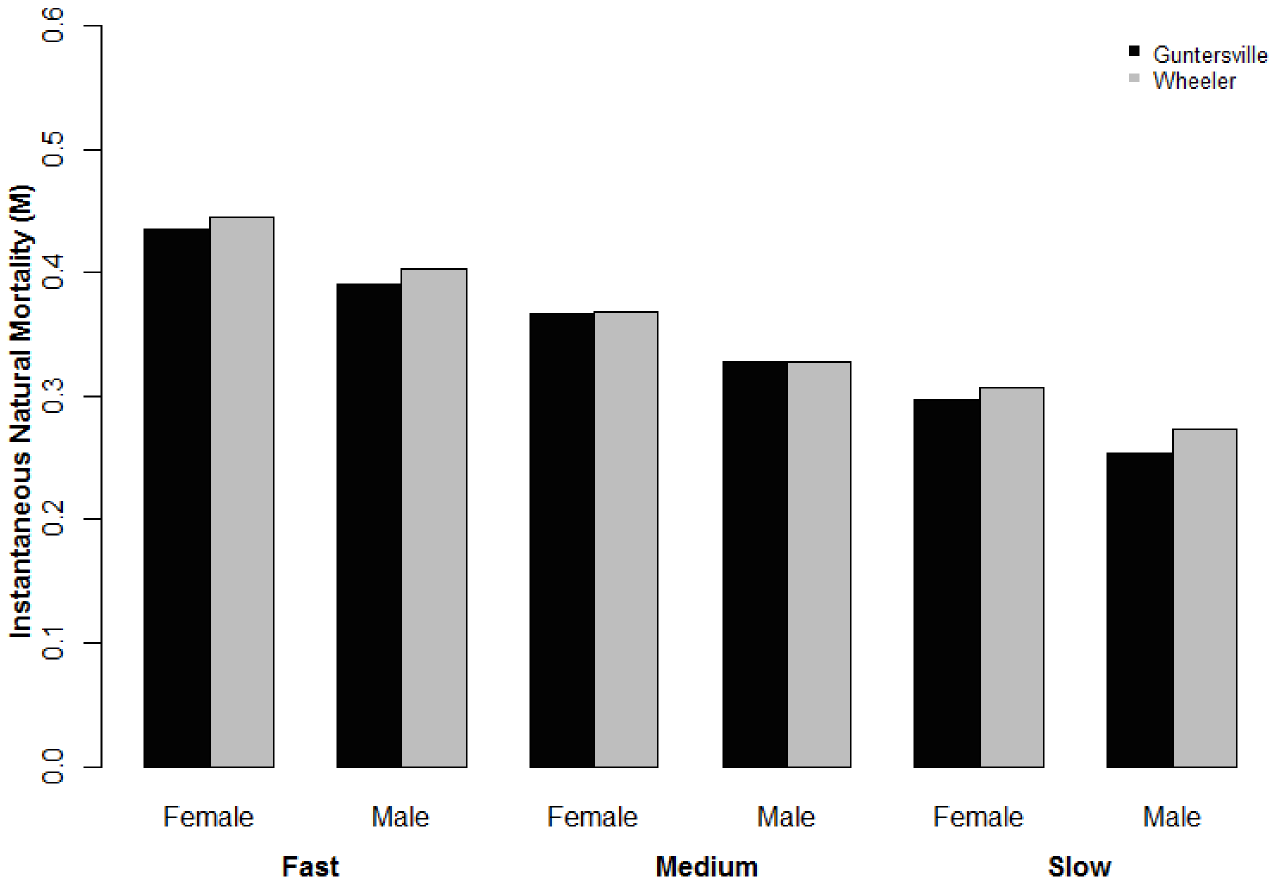
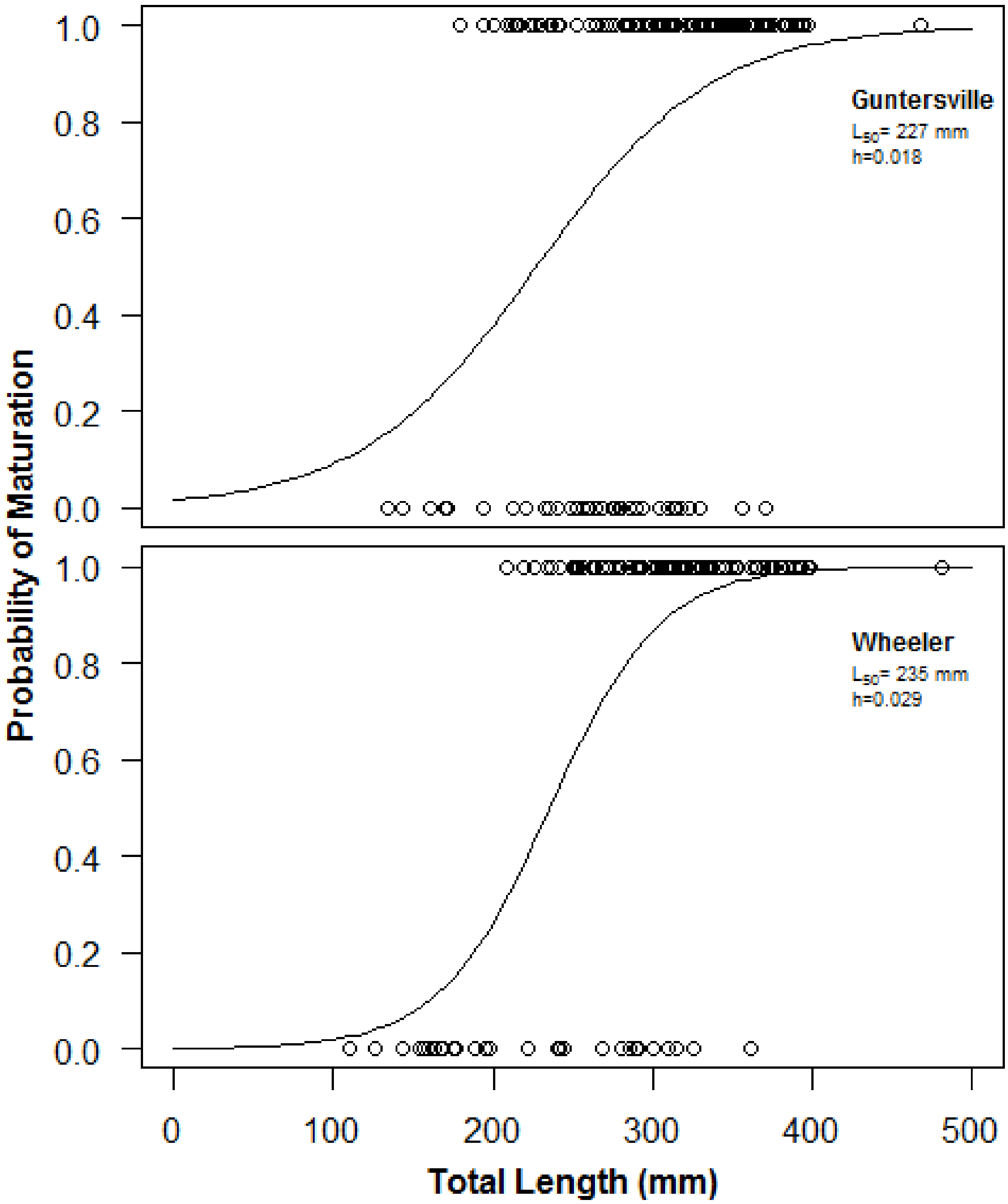


Figure 12.



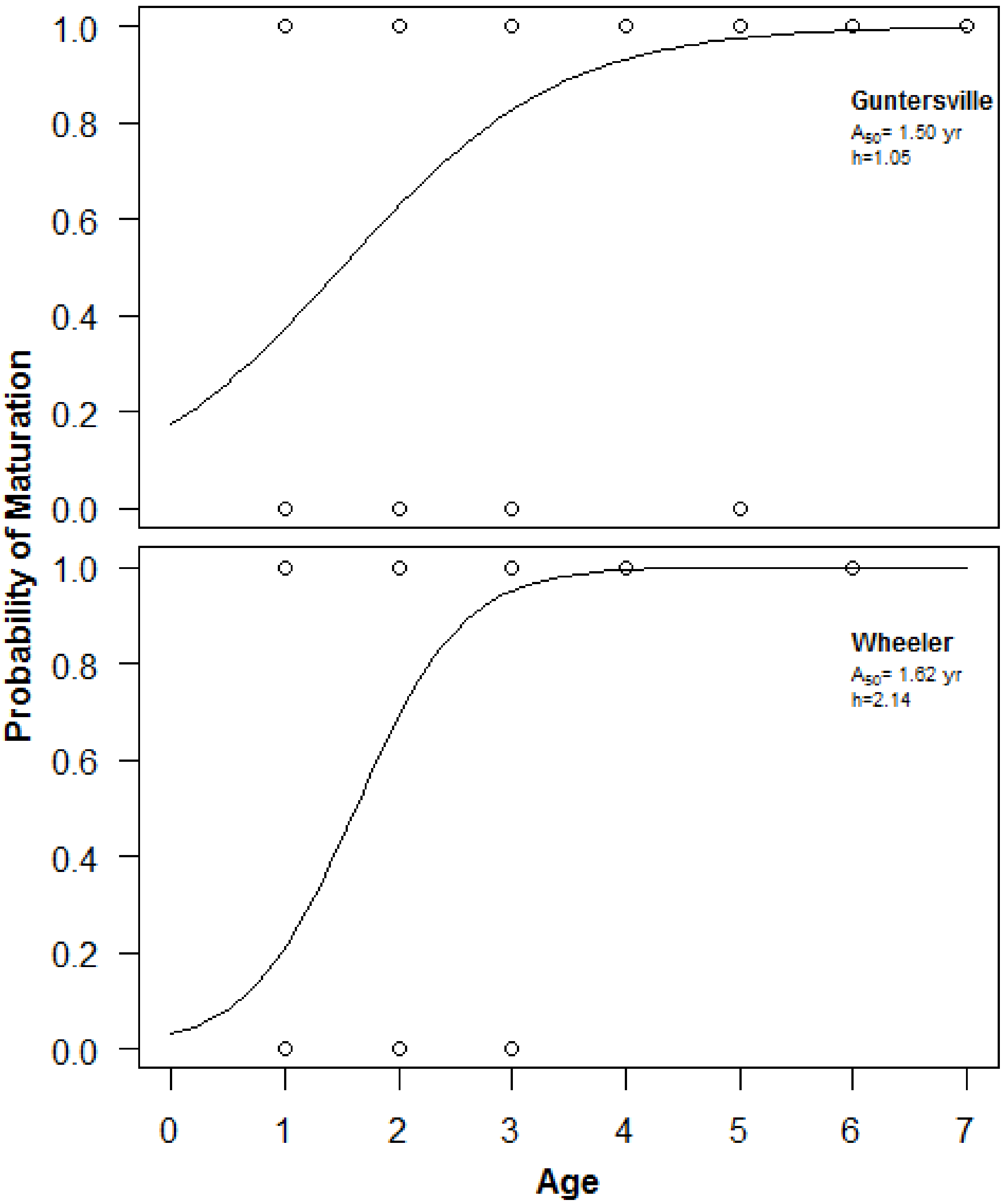
Instantaneous Natural Mortality (M)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
■ Guntersville
■ Wheeler
Female
Male
Female
Male
Female
Male
Fast
Medium
Slow

Figure 13.



Probability of Maturation
1.0
0.8
0.6
0.4
0.2
0.0
Guntersville
L_{50}= 227 mm
h=0.018
Wheeler
L_{50}= 235 mm
h=0.029
0
100
200
300
400
500
Total Length (mm)

Figure 14.



1.0
0.8
0.6
0.4
0.2
0.0
Probability of Maturation
Guntersville
A_{50}= 1.50 yr
h=1.05
Wheeler
A_{50}= 1.62 yr
h=2.14
0
1
2
3
4
5
6
7
Age

Figure 15.

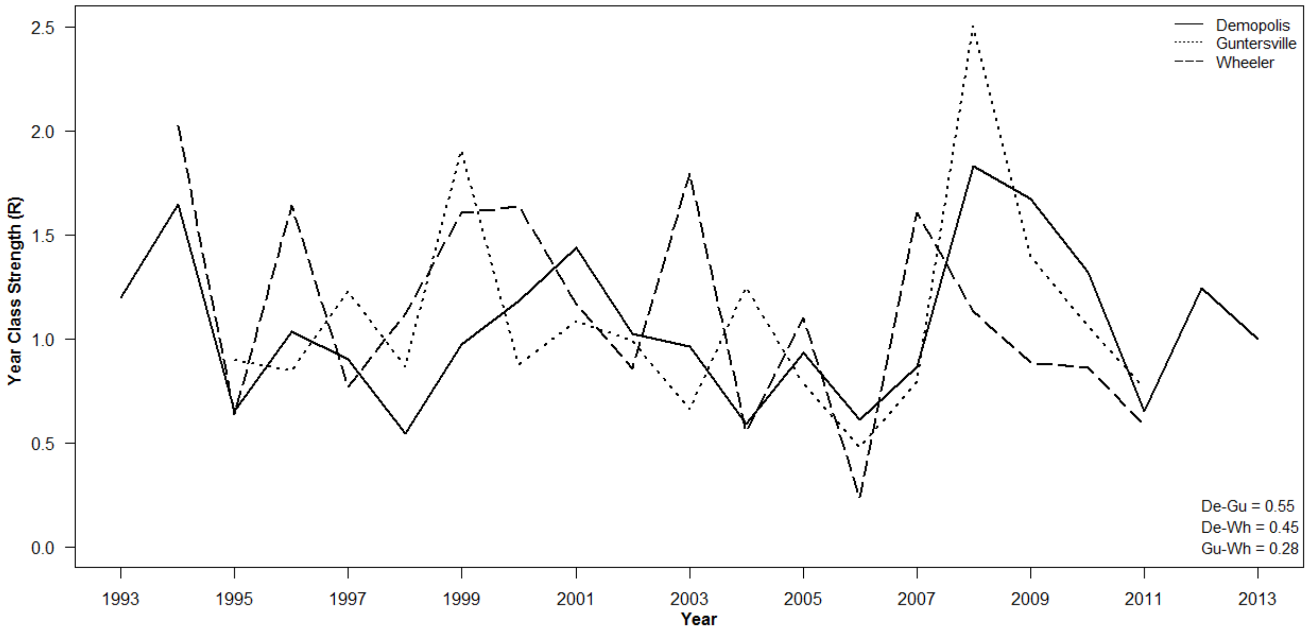

Demopolis
Guntersville
Wheeler
De-Gu = 0.55
De-Wh = 0.45
Gu-Wh = 0.28
Year Class Strength (R)
0.0
0.5
1.0
1.5
2.0
2.5
Year
1993
1995
1997
1999
2001
2003
2005
2007
2009
2011
2013

Figure 16.

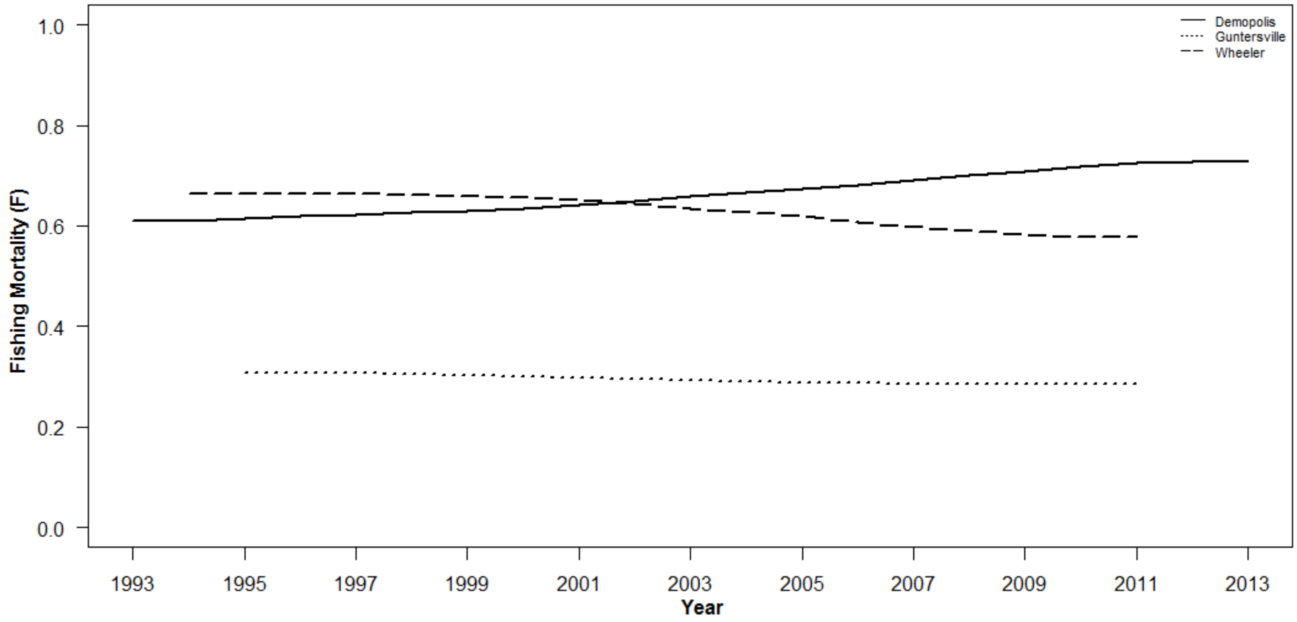

Demopolis
Guntersville
Wheeler
Fishing Mortality (F)
1.0
0.8
0.6
0.4
0.2
0.0
1993
1995
1997
1999
2001
2003
2005
2007
2009
2011
2013
Year

Figure 17.

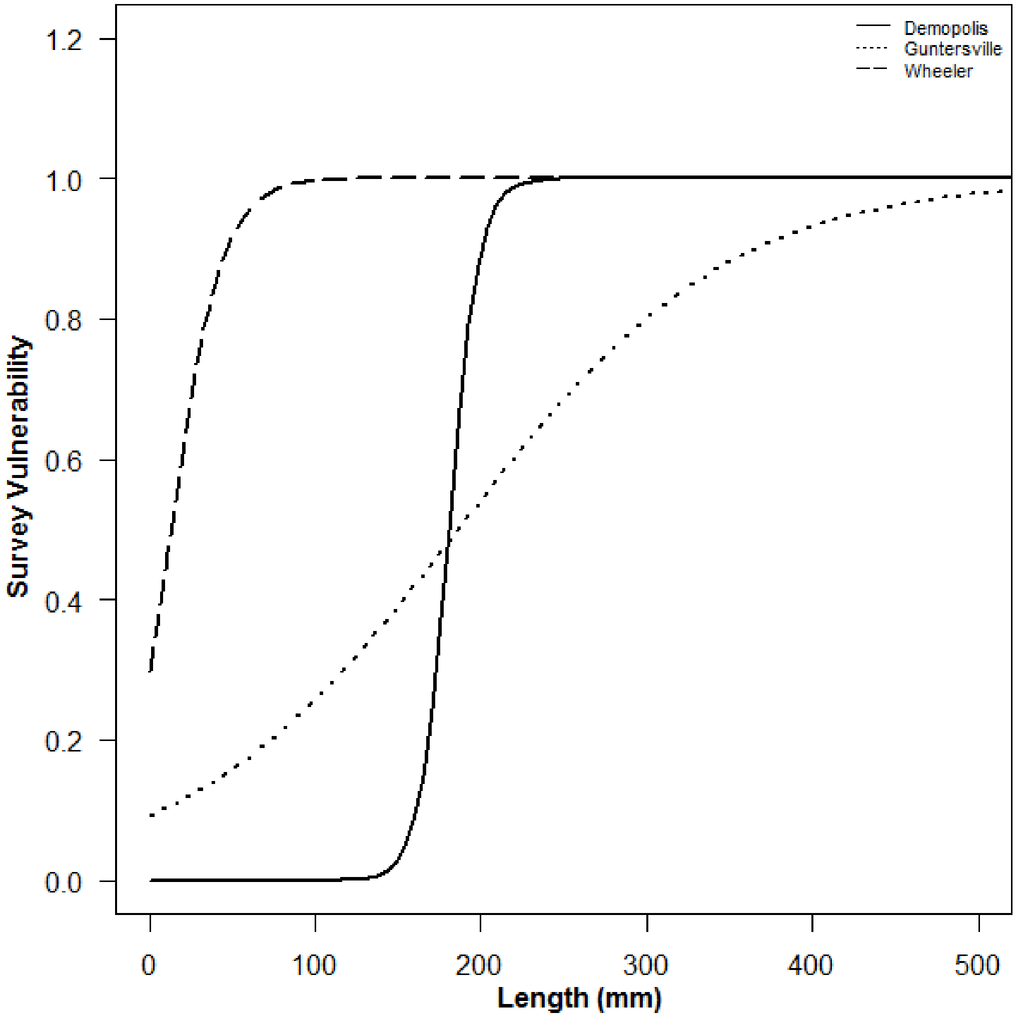

Demopolis
Guntersville
Wheeler
Survey Vulnerability
0.0
0.2
0.4
0.6
0.8
1.0
1.2
0
100
200
300
400
500
Length (mm)

Figure 18.

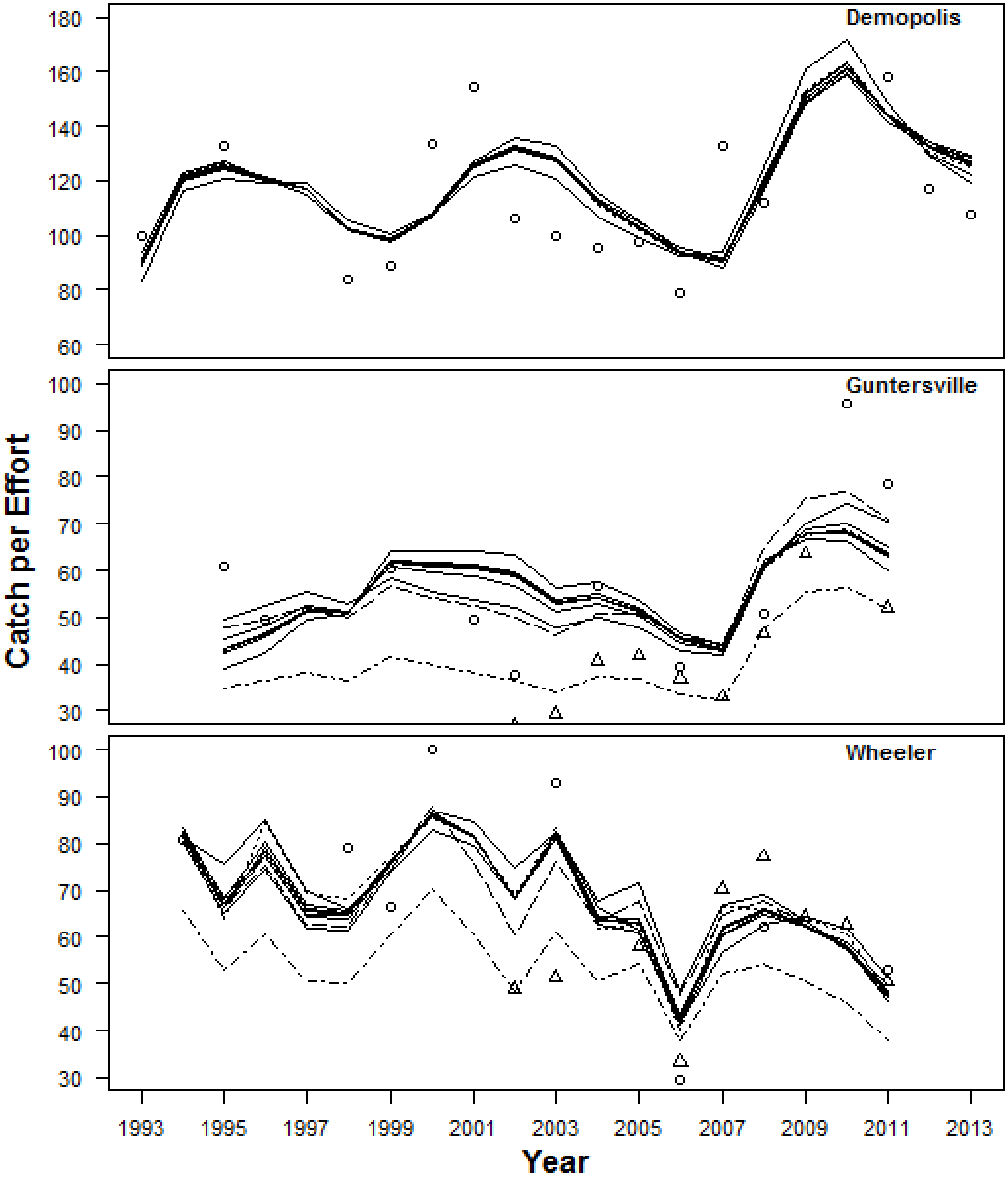

Demopolis
Guntersville
Wheeler
Catch per Effort
Year
180
160
140
120
100
80
60
100
90
80
70
60
50
40
30
100
90
80
70
60
50
40
30
1993
1995
1997
1999
2001
2003
2005
2007
2009
2011
2013

Figure 19.

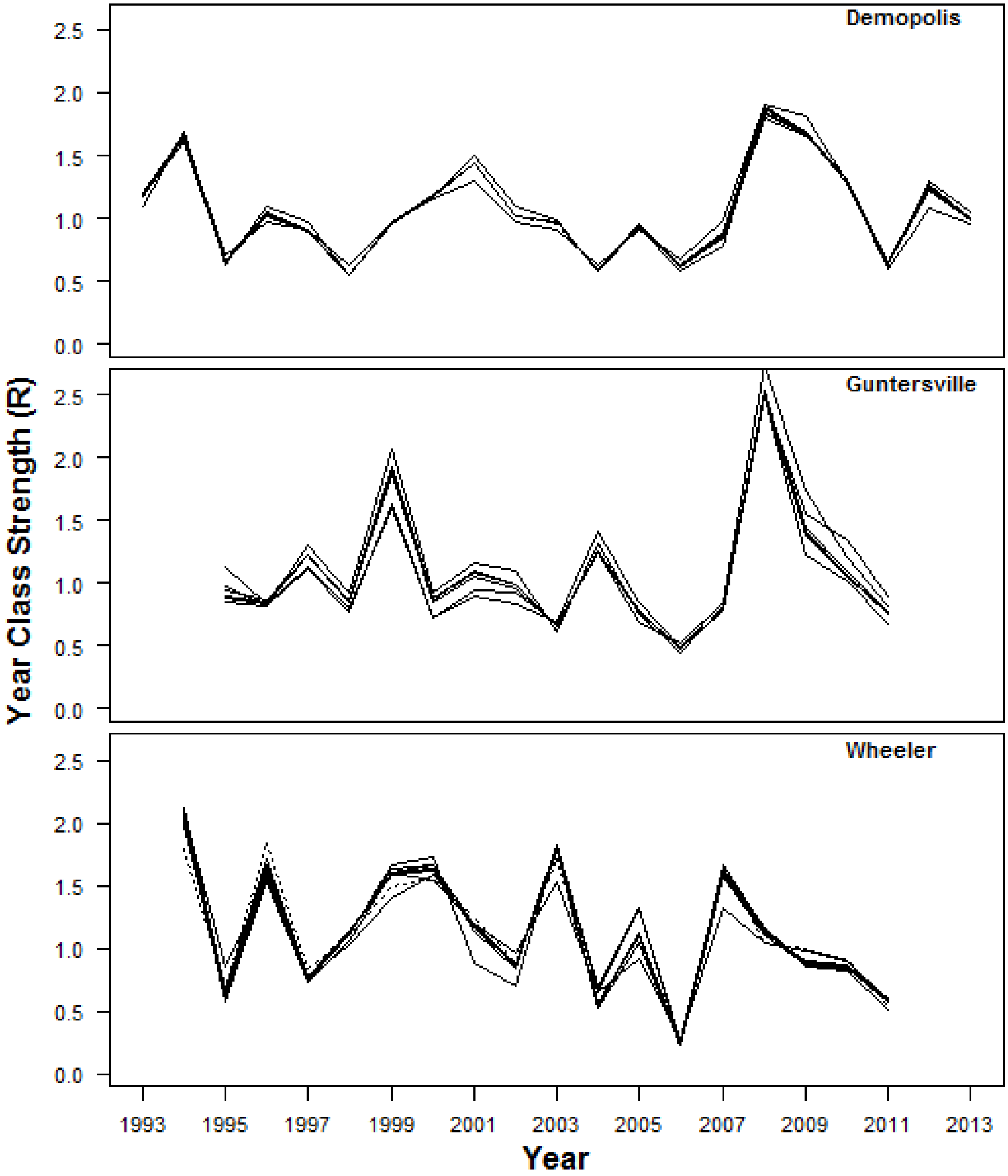

Demopolis
Guntersville
Wheeler
Year Class Strength (R)
0.0
0.5
1.0
1.5
2.0
2.5
1993
1995
1997
1999
2001
2003
2005
2007
2009
2011
2013
Year

Figure 20.

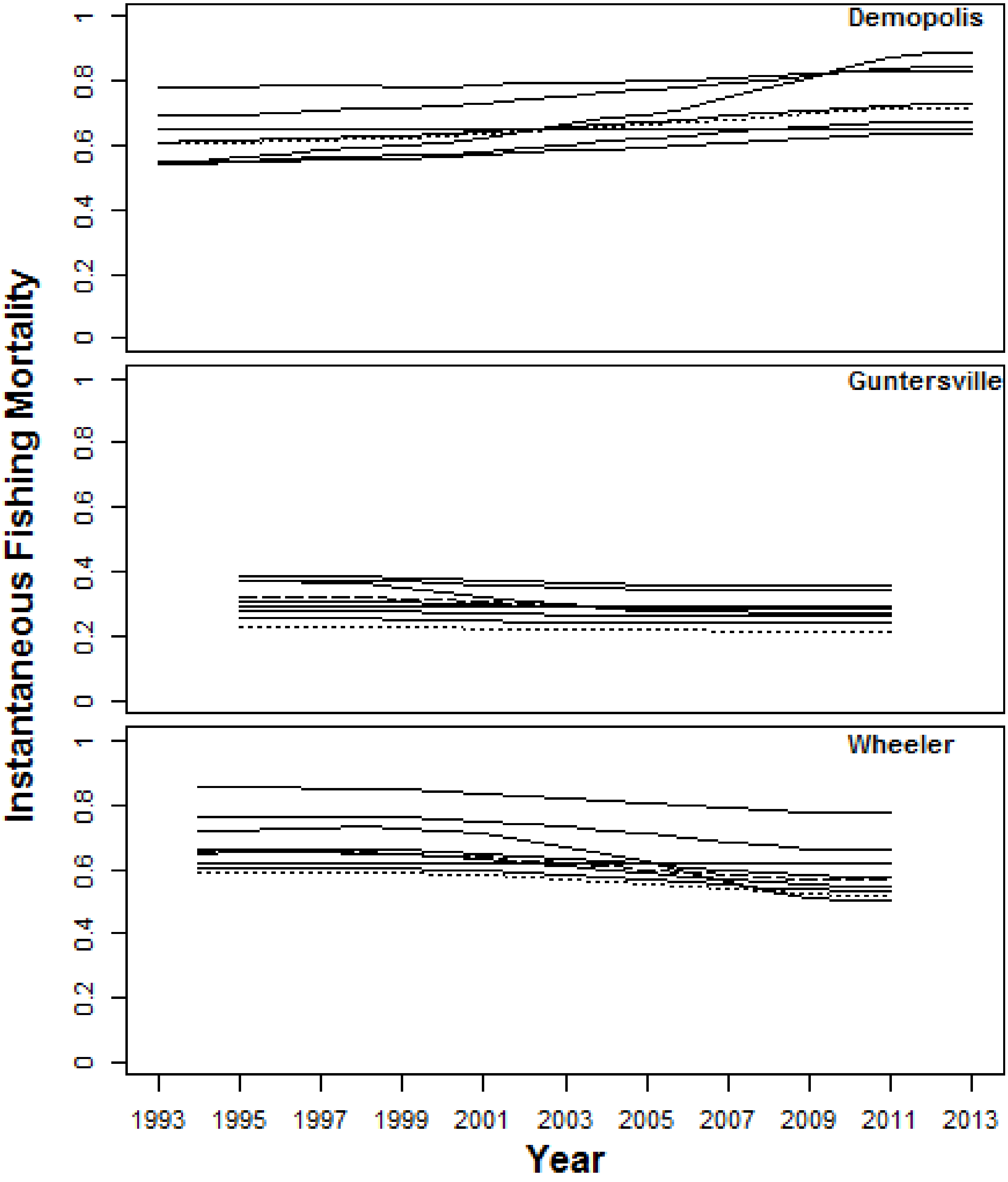

Demopolis
Guntersville
Wheeler
Instantaneous Fishing Mortality
0
0.2
0.4
0.6
0.8
1
1993
1995
1997
1999
2001
2003
2005
2007
2009
2011
2013
Year

Figure 21.

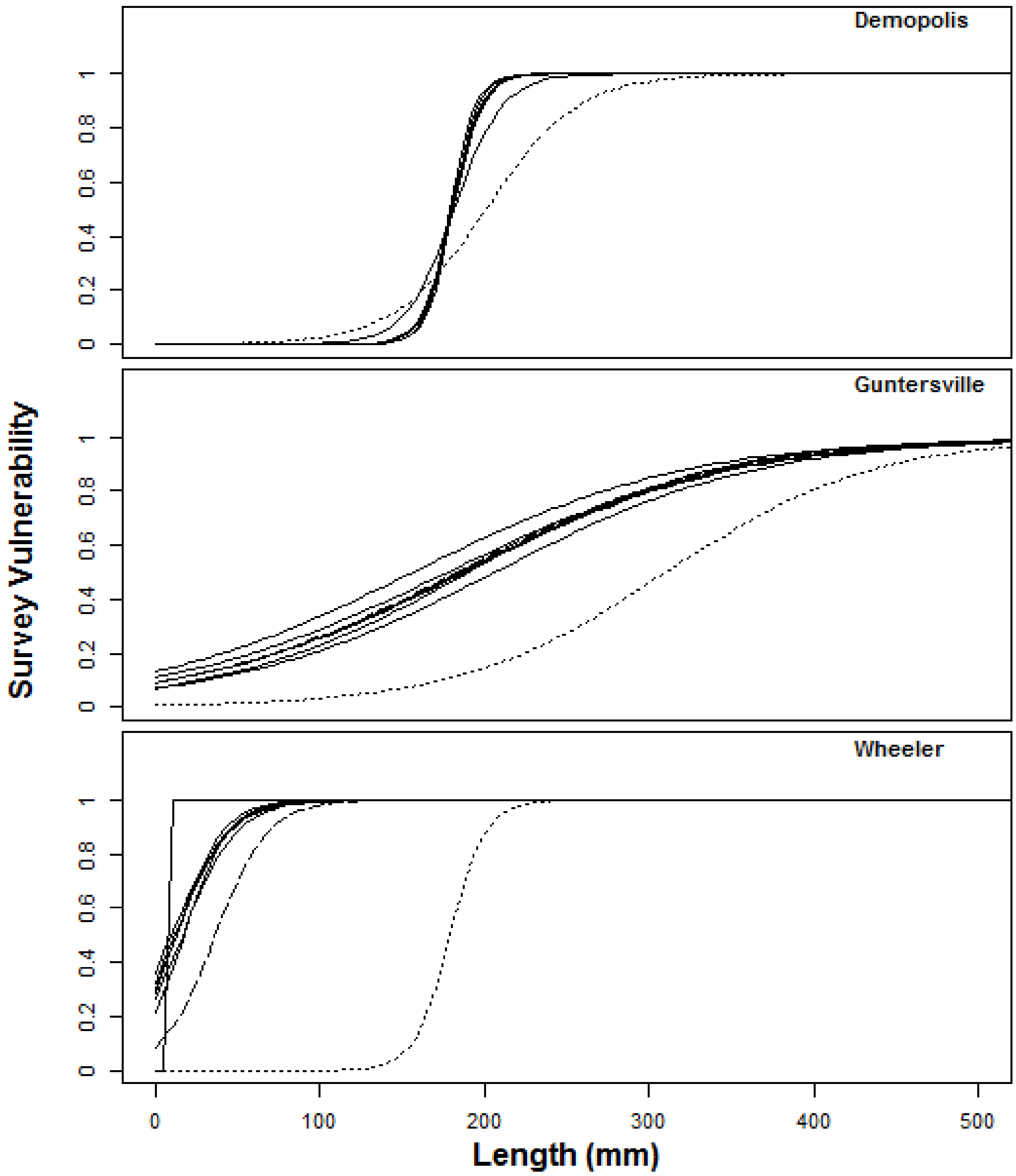
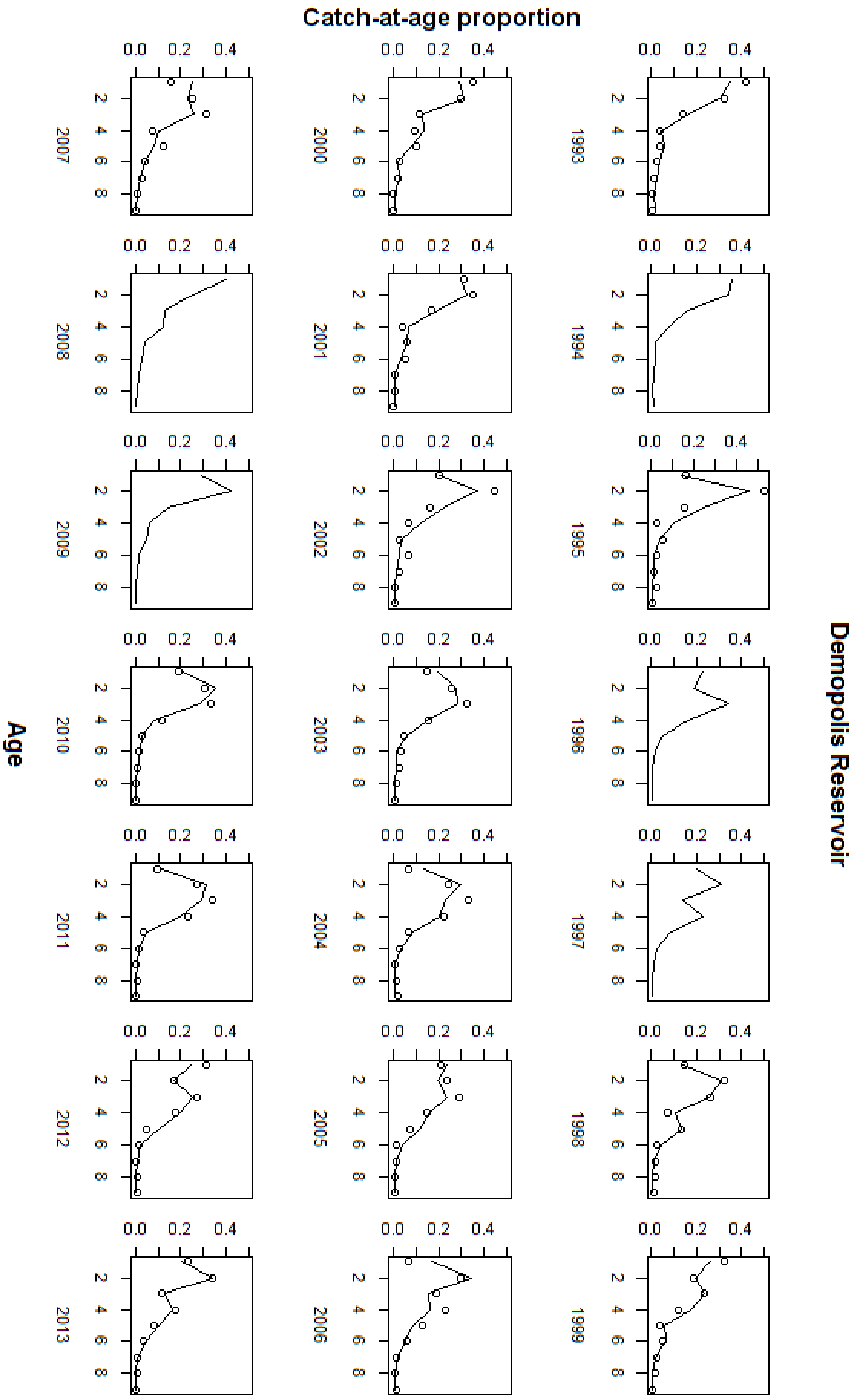
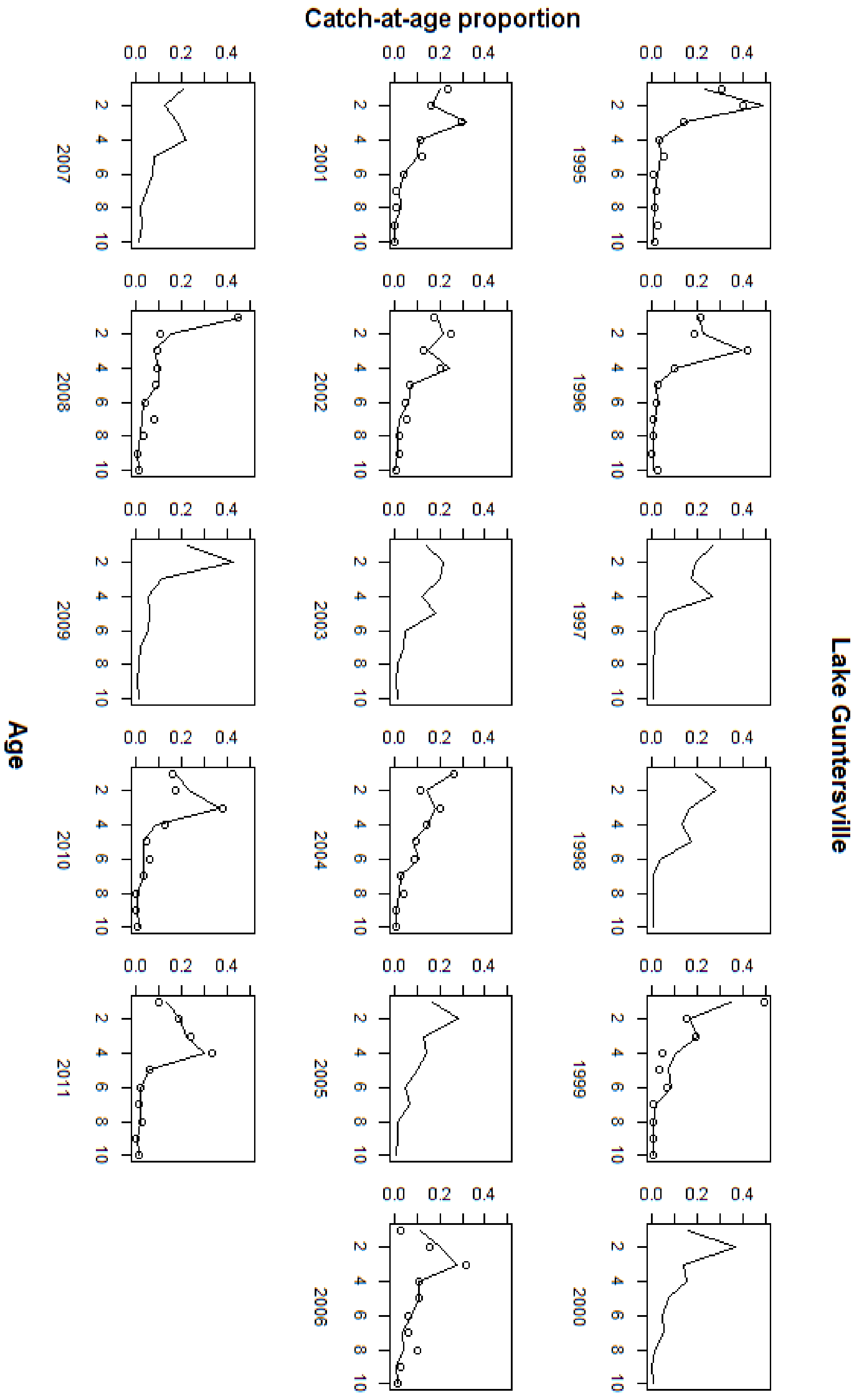
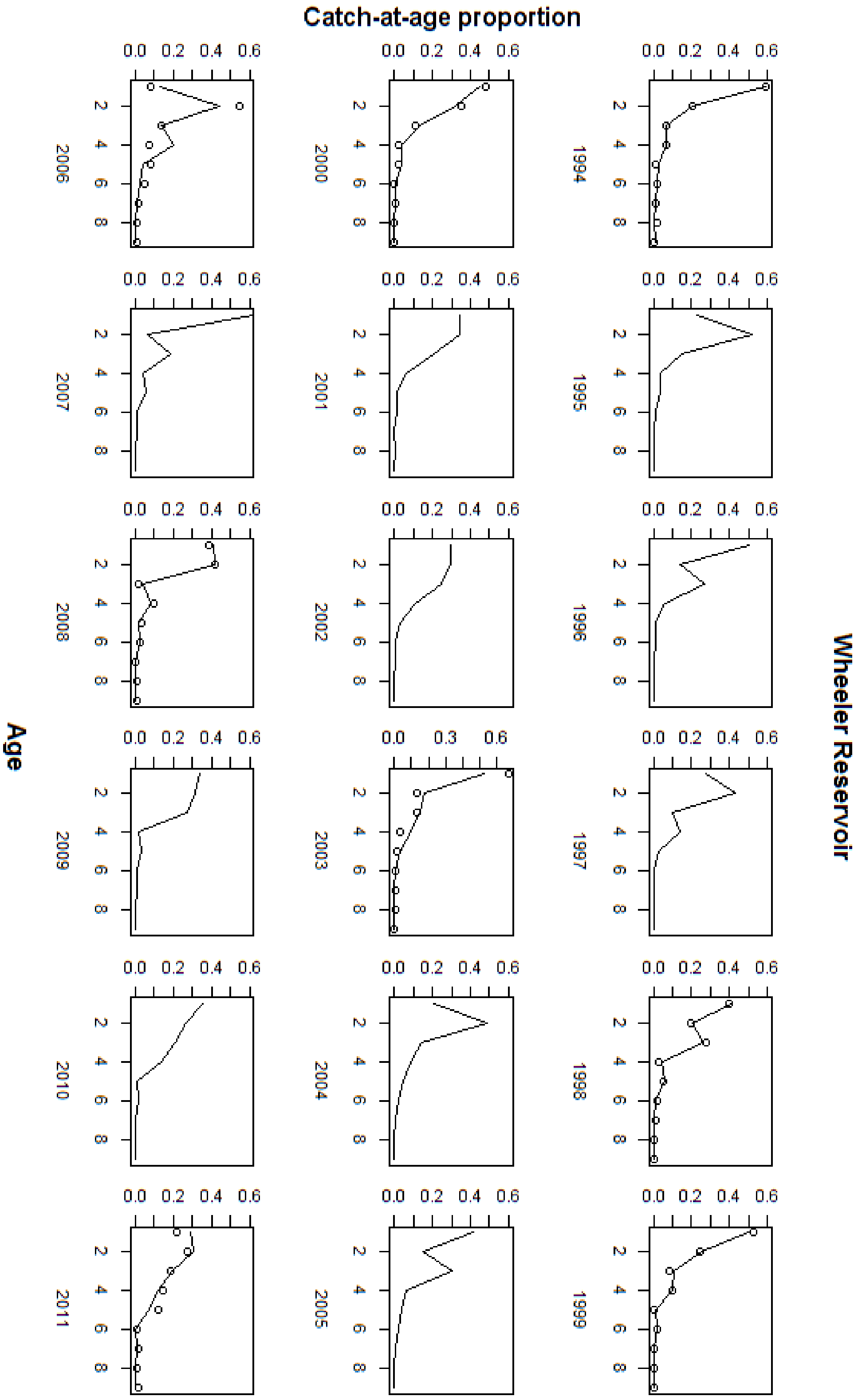

Demopolis
Guntersville
Wheeler
Survey Vulnerability
0
0.2
0.4
0.6
0.8
1
Length (mm)
0
100
200
300
400
500

Figure 22.

Appendix A.


Catch-at-age proportion
Demopolis Reservoir
Age
0.0
0.2
0.4
2
4
6
8
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013


Catch-at-age proportion
Age
Lake Guntersville
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
0.0
0.2
0.4
2
4
6
8
10


Catch-at-age proportion
Age
Wheeler Reservoir
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
0.0 0.2 0.4 0.6
0.0 0.3 0.6
2 4 6 8