Developing Biological Reference Points and Identifying Stock Status for Management of Paddlefish (*Polyodon spathula*) in the Mississippi River Basin

Final Report

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by

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Executive Summary

Paddlefish (*Polyodon spathula*, *Polyodontidae*) is commercially and recreationally important throughout much of the Mississippi River drainage. There is growing concern about the status of major stocks, primarily due to recent increase in demand for Paddlefish roe, as well as increased popularity of Paddlefish as an target of the recreational fishery. Significant increase in fishing pressure in the absence of clear management goals to ensure sustainability could lead to recruitment overfishing and population collapse. The goal of this study was to assemble and critically review existing biological information, landings, indices of abundance, modeling and management approaches to identify sustainable rates of exploitation, develop biological reference points, and provide management and research recommendations. In the course of this study we complied published estimates of growth parameters, length – weight relationship, maturity schedule, fecundity, natural mortality. Several sets of parameters were directly estimated for the stocks where raw data were available.

Growth of Paddlefish is generally the best researched portion of the population dynamics, both geographically and by sex. All available data sets have shown statistically significant differences in growth rates between males and females with females growing generally faster and achieving larger asymptotic size. Populations from different geographic regions show substantial differences in their growth patterns, but very few data sets were available for formal testing. Overall evidence suggests presence of sex and region specific differences that are perceived to be determined by sex specific life history parameters and aquatic ecosystems productivity. We characterized variability in size at age and used it to calculate fishery selectivities for various minimum size management scenarios. Weight at size also differs by region and sex. Growth differences are likely to have significant effect on individual weight at age, total biomass production and population fecundity and should be accounted for in calculation of reference points.

We described maturity as a function of both age and size where possible. Maturity schedules were significantly different among stocks with available data. The fraction of gravid females reaches 100% for some stocks at a large size or age, while females in some stocks never reach 100% gravidity, suggesting that some fraction of females does

not spawn annually. Female fecundity was moderately correlated with size, higher correlation with weight than length, while relative fecundity (number of eggs per kg of body weight) was fairly constant.

Natural mortality is the most influential parameter for estimating stock productivity and resilience to fishing. Natural mortality rate estimates were produced using a range of methods that were based on life history traits. Estimated natural mortality values varied substantially for each stock, as well as among the stocks. The best group of methods for natural mortality estimation are those based on maximum life expectancy. The least uncertain and the lowest (M= 0.05-0.07) natural mortality values were estimated for the most northern stocks with extended age structure (Yellowstone River and Upper Missouri River). Stocks in the center of distribution appeared to have higher natural mortality (M = 0.14-0.2) indicated by a lower maximum age, but the lower maximum age is likely caused by exploitation. Natural mortality of stocks in the center of distribution is likely to be similar to those of the more northern populations, which is corroborated by a few direct estimates based on tagging studies. Natural mortality of stocks in the southern range appear to be the highest (M =0.2 – 0.3).

Total mortality rates were estimated using year-class curves, year-specific catch curves, and a length-based catch curve approach for 14 systems. Total mortality rate estimates were generally high, but varied across systems. Lake Francis Case had the lowest total mortality rate estimate at 0.18 per year, while the Arkansas River had the highest estimates at 1.35 per year. After accounting for natural mortality, estimated fishing mortality rates substantially exceeded $F_{40\%}$ in most systems.

Yield per recruit (YPR) and spawning potential ratio (SPR) analyses were completed for a number of stocks representing a range of growth, maturity, natural mortality, geography and habitat. The analyses were completed for a range of minimum legal sizes used as regulatory tool. With a few exceptions, YPR increases monotonically with the increase in fishing mortality (there is no maximum for YPR). As a result, the maximum fishing mortality should be defined by the fishing mortality level that provides sustainable reproduction based on SPR.

Elasticity analysis was applied to several stocks representing a range of age structures, maturity schedules and mortality rates. Elasticity results indicated that growth

rate of all populations was most sensitive to the survivorship of immature fish. Survivorship of mature fish had smaller effect, and survivorship of eggs was least influential. These results suggest that when restoration efforts are underway, improvements in survivorship of immature fish will provide the strongest population response.

Although basic life history parameters for most stocks are sufficiently described, the fishery dependent information such as time series of catch, indices of abundance or systematic age and size structure data are very limited or absent. Lack of sufficient time series of basic fishery dependent data qualifies most Paddlefish stocks as "data poor." Due to these limitations, attempts to apply fishery models that require catch information, catch and an index of abundance (surplus production models), or catch combined with age structure and indices of abundance (statistical catch at age models) were not possible. However, at least two stocks appear to have the data necessary to apply modern, age-structured assessment methods, but the data were not available to the assessment team. Data limitations severely restricted ability to estimate current fishing mortality or stocks abundance and biomass. Recruitment estimates are also not available, but some data suggest that some exceptionally strong year classes have been observed infrequently.

A range of potential biological reference points was considered for management purposes. It was not possible to recommend biomass reference points due to the lack of biomass estimates. Currently only fishing mortality reference points are recommended. There are no estimates of fishing mortality corresponding to the maximum sustainable yield (F_{MSY}) available and none were estimated in this study due to data limitations. Several approaches for estimating proxies of F_{MSY} suggested that fishing mortality values corresponding to 30 and 40% spawning potential of the unfished population ($F_{30\%}$ and $F_{40\%}$) are suitable as limit and target reference points. Management recommendations for data poor situations and research recommendations for improving data collection of critical fishery information are proposed.

1. Introduction

American Paddlefish (*Polyodon spathula*, *Polyodontidae, hereafter Paddlefish*) is a large fish that is endemic throughout much of the Mississippi River drainage and adjacent Gulf slope drainage in North America (Burr, 1980). Paddlefish were historically harvested primarily for their flesh, but the importance of Paddlefish as a major domestic source of eggs for caviar increased during the late 1800s (Jennings and Zigler, 2009). Commercial Paddlefish landings reached a peak in the early 1900s and declined thereafter with a series of fluctuations throughout their range. The primary reasons for the decline in abundance and commercial harvest are believed to be overfishing and habitat degradation (Scholten, 2009). The number of states listing Paddlefish as endangered, threatened, or a species of concern increased from five states in 1983 to 11 states in 1994 (Graham, 1997). Concern for Paddlefish populations prompted the U.S. Fish and Wildlife Service (USFWS) to recommend that Paddlefish be protected through the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). The addition of Paddlefish to Appendix II of CITES in 1992 provided a mechanism to curtail illegal trade in Paddlefish products (USOFR, 1992). A recent review of Paddlefish status (Bettoli et al., 2009) indicated that most Paddlefish populations in most states within the Mississippi River basin were relatively stable. However, there is a rising trend in Paddlefish caviar production due to increasing demand, following the precipitous decline of Caspian Sea sturgeon populations. The potential for increased fishing pressure in the absence of clear management goals could lead to recruitment overfishing and population collapse.

Managing for a sustainable fishery requires detailed knowledge of fishery removals, population dynamics, and productivity. Despite multiple studies of Paddlefish biology, no estimates of sustainable and optimum exploitation rates have been developed to date. State-specific fishing regulations vary and are not based on a unified management methodology. Currently, very few estimates of fishing mortality are available for local stocks, and there are no clearly determined biological reference points that define targets or limits for population size and fishing mortality rates for management purposes. Effective management of the fishery is not possible without established targets for sustainable Paddlefish population sizes, associated sustainable fishing mortality rates, and methods to compare the state of the population to those targets. Current estimates of fishing mortality and stock sizes are required to make appropriate management decisions. Without such measures

Paddlefish may experience a serious risk of overfishing and potential commercial and biological extinction.

To bridge the gaps in current scientific approaches to Paddlefish fishery management, we critically reviewed the relevant literature on Paddlefish life history and completed quantitative analyses of available data on growth, maturity, fecundity, and estimated natural and total mortality rates. Life history parameters for various stocks were summarized or developed where new data were available. Estimated biological parameters were used as inputs into models intended to inform fishery managers about the possible range of sustainable exploitation levels given stock specific productivity, nature of the fishery (commercial, recreational, or both), and management goals. Following the modeling results, we provided recommendations on sustainable levels of Paddlefish exploitation. Identified targets and limits can be directly adopted by states for their management programs. Alternatively, the states can consider them as a starting point and proceed with their own modifications. At a minimum, the results of the analysis will provide guidance for establishing a scientifically sound and responsible management regime for Paddlefish in the U.S.

2. Life History Parameters

2.1. Geographic Range

Historically, Paddlefish were abundant throughout the Mississippi River basin and adjacent Gulf of Mexico coastal drainages, and once were found in some of the Great Lakes and Canada (Gengerke, 1986; Graham, 1997). Over the past century, their range has shrunk, and the relict population in the Great Lakes has been lost (Figure 2.1.1). Paddlefish are currently found in 22 states (Figure 2.1.2), primarily in low velocity rivers and associated lakes of the Mississippi River and Mobile Bay drainages. Their current range spans from the Missouri and Yellowstone Rivers in the northwest to the Ohio and Allegheny Rivers of the northeast; from the headwaters of the Mississippi River south to its mouth; and from the San Jacinto River in the southwest to the Tombigbee and Alabama Rivers of the southeast (Jennings and Zigler, 2000). Overall, historical and current distributions of Paddlefish are well described in the literature at various geographic scales, both nationally and regionally.

Habitat alterations (as a result of human activities) are the principal reasons for the contraction of species distribution. Construction of a large number of dams throughout the Mississippi River drainage has limited the ranges of many populations of Paddlefish. Due to these blockages, migratory breeding behavior has been disrupted, and many spawning areas previously sustaining Paddlefish were lost (Graham, 1997; Mims, 2001). In addition, channelization and elimination of backwater areas, destruction of spawning grounds, dewatering of streams, industrial pollution, and overharvest have all contributed to the extirpation of some local stocks.

Several aspects of Paddlefish distribution are relevant to the goal of establishing a scientifically sound management. Their extensive geographic range, in particular latitudinally (north-south), indicates adaptability of Paddlefish to a wide variety of environmental conditions, especially the temperature range, zooplankton productivity cycles, and the duration of a growing season. Variability in ecotopes occupied by Paddlefish, specifically riverine (mainstem) and lacustrine (natural lakes and reservoirs) environments is another factor contributing to differences in population productivity and life history parameters. Differences in environmental conditions can have significant effects on growth, maturity, fecundity and mortality rates leading to potentially significant differences among local stocks regarding productivity and resilience to fishing pressure.

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2.2. Movements

Paddlefish are considered to be highly mobile and are capable of making extensive movements (Rosen et al., 1982; Southall and Hubert, 1984; Russell, 1986; Moen, 1989, Jennings and Zigler, 2000). The most frequently documented Paddlefish movements occur in the spring as Paddlefish move upstream towards spawning areas (Purkett, 1961; Rehwinkel, 1978; Southall and Hubert, 1984, Firehammer and Scarnecchia, 2006). Spawning migrations of more than 333 km upstream were common in the Osage River, Missouri (Russell, 1986). On some occasions, Paddlefish were observed to make their spawning migration in large aggregations (Stockard, 1907; Meyer, 1960). Paddlefish were also reported to have substantial movements not related to spawning, both in upstream and downstream directions. Rosen et al. (1982) reported that tagged fish travel up to 50 km upstream to the tailwater of the dam on Missouri River, while the average downstream distance traveled was 147 km. Some fish traveled more than 200 km downstream and one tagged fish was recaptured nearly 2000 km downstream.

Although multiple dams can be barriers to movements of Paddlefish (Southall et al., 1984; Russell, 1986; Moen et al., 1992), some Paddlefish are capable of upstream movements. These movements primarily occur through the low head navigation dams. Under certain conditions downstream movement through partially open roller gates can occur without the fish experiencing major injury (Gengerke, 1978; Southall and Hubert, 1984; Moen et al., 1992; Jennigs and Zigler, 2000). Dams can isolate and confine Paddlefish (Russell, 1986), but extensive within-pool movements still occur (Rosen et al., 1982; Southall, 1982; Moen, 1989; Zigler et al., 1999).

The most extensive analysis of Paddlefish movements was completed by Pracheil et al., (2012), who quantified intrajurisdictional (within a state) and interjurisdictional (between states) movements of Paddlefish at multiple spatial scales by enumerating movements of wild and stocked Paddlefish using the Mississippi River Interstate Cooperative Resource Association (MICRA) tagging database. This database contains mark–recapture and biometric information on more than 30,000 individually marked wild Paddlefish and more than 2 million hatchery-origin Paddlefish. Despite the large total number of recovered tags, the data proved to be too sparse to allow state specific estimates of movement. Consequently, movement was quantified for four river basins, as designated in MICRA database – Gulf, Mississippi, Ohio and Missouri. Most movements (61%) of wild Paddlefish (as determined by state of initial capture and state of recapture) occurred within a single state (Pracheil et

al., 2012). However, 39% of movements of wild Paddlefish occurred across state boundaries with movements out of river basins accounting for 2% of inter-jurisdictional movements and 1% of total movements (Table 2.2.1). No movements were recorded to or from the Gulf Basin, likely due to the absence of freshwater connections. Wild Paddlefish movements appear to be generally confined within a river basin at annual scales. Interbasin movements were most common from the Missouri to Mississippi basin and the reciprocal. Interbasin movements also occurred from the Mississippi to the Ohio basin, but not the reciprocal. Overall, the movements generally occurred between bordering states (Table 2.2.1), and the probability of Paddlefish remaining within the same basin was very high for all four basins: 0.9994 for the Ohio, 0.9897 for the Mississippi, 0.9987 for the Missouri and 1.0 for the Gulf. This finding suggested that Paddlefish stocks could be considered as separate units for management purposes, at least on the basin scale. These differences should be accounted for in estimation of life history parameters and development of references points for management.

2.3. Age determination and validation

Age determination in Paddlefish has been conducted using several hard body parts such as fin rays, otoliths, and lower jaw bones or dentaries (Adams, 1942; Meyer, 1960). However, fin rays were shown to be inadequate for determining the age of Paddlefish because adjacent fin rays do not always have the same number of annuli (Meyer, 1960). Otoliths provide reliable estimates for younger fish, but crowding of the annuli make it difficult to use of otoliths for age determination of older fish (Adams, 1942; Meyer, 1960). Currently, the preferred structure for aging is the dentary bone because of reduced false annuli and comparatively large inter-annular distances for older fish (Adams, 1942; Meyer, 1960; Scharnecchia et al., 1996; Figure 2.3.1). This method of age determination has been used throughout the range of Paddlefish distribution including the Illinois River (Adams, 1942), Montana and North Dakota for the Yellowstone–Sakakawea stocks (Scarnecchia et al. 1996), Lake Francis Casein South Dakota (Pierce et al., 2011), Lakes Barkley and Kentucky in Tennessee (Bronte and Johnson, 1985; Scholten and Bettoli, 2005), the Arkansas River in Arkansas (Leone et al., 2011), Grand Lake in Oklahoma (Scarnecchia et al., 2011), the Atchafalaya River and two lakes in Louisiana (Reed et al. 1992), and many other locations. However, very few studies of Paddlefish age and growth have addressed the accuracy and potential bias of ages determined from dentary bones. Preparation techniques, age reading protocol, and skills of individual readers can significantly affect age reading quality (Meyer, 1960; Alexander et al., 1985; Campana, 2001).

To address an individual reader effect, aging by two readers is becoming a standard practice to ensure quality control. The process requires two readers to independently age dentary cross sections and compare their results. When ages do not agree after the initial reading, fish are aged again by both readers in consultation and final ages are assigned by the primary reader. This process has been used with variations in ageing Paddlefish from the Yellowstone River and Sakakawea Lake (Scarnecchia, et al., 2006), Grand Lake in Oklahoma (Scarnecchia et al., 2011), the Arkansas River (Leone et al., 2011), Lake Francis Case (Pierce et al., 2011), and the lower Mississippi River (Tripp et al., 2012).

Several studies used known-age Paddlefish to estimate aging accuracy. Quinn et al. (2006) assessed the validity of the double-blind procedure to age Paddlefish (6 to 10 years of age) collected from Harry S. Truman and Table Rock Lakes, Missouri. Estimated ages were compared to the known ages of Paddlefish. Forty-one percent of ages (N = 44) were accurately assigned using the double-blind procedure and 84% of ages were within one year (Figure 2.3.2). Most errors of over 1 year were

associated with jaw bones that had a high degree of haloing or jpeg images that were too dark and masked at least one annuli. Quinn et al. (2006) concluded that aging Paddlefish with dentary bones appears to produce reasonable and unbiased ages. However, there was some indication of underestimation for the oldest age group (age 10, see Figure 2.3.3), but old Paddlefish were not represented in the study. Pierce et al. (2011) were able to accurately estimate the age only for 8.6% of the fish aged. Fifty percent of dentary ages were within one year of true age, 74% were within two years, and 91% were within three years. More importantly, there seemed to be a significant age underestimation starting with age 8 (Figure 2.3.4).

The largest evaluation to date was conducted by Scharnecchia et al. (2006), who attempted to validate the accuracy and precision of age estimates for the Yellowstone – Sakakawea stock in Montana and North Dakota. Twenty-five of 30 fish (age range 7 to 10) tagged with coded wire tags as age-0 fish were aged correctly with dentaries. Estimates for the other five fish (16.7%) deviated from actual ages by one year. The coefficient of variation for age estimates was reported in the range of 3.6-7.2%, indicating high age-reading precision. However, no estimate was produced for aging precision by the same reader and no precision estimates were available for fish older than age 10 (no known-age fish were available for validation).

For fish older than age 10, estimated ages were compared with the estimated minimum potential ages (i.e., times at large) of recovered fish that were jaw-tagged. Ninety-three percent of the sample (323 fish) had estimated ages that were the minimum potential age or older. For a small percentage of the sample (7%), the age was underestimated (fish were aged less than the minimum expected ages). The authors concluded that *"The results indicate that estimating ages from Yellowstone–Sakakawea Paddlefish dentaries is generally a repeatable, straightforward process with sufficient accuracy and precision to be useful for stock assessment."* While the age validation for fish up to age 10 appears to be convincing, the results are not as conclusive for older fish. The comparison only demonstrated that the estimated age was at least equal or greater than the number of years at large (time between the moment of tagging and the moment of recovery). However, since the true age of tagged fish was not known, the estimated age could still differ from true age, resulting in aging bias.

Age determination using lower jaw bones appears to be well established. Two-reader techniques designed to reduce individual reader error are becoming a standard practice. Reported precision estimates vary substantially by study from very precise (83%) to low (8.6%). There appears to be a high chance of underestimation of age for ages 10 and older. Negative bias may substantially

affect the results of stock assessments when age-specific information is utilized. Therefore, it is advisable to expand on the current validation studies to quantify age reading errors for precision and bias for any stock where the assessment of the status of the stock and management actions rely on age information. These studies should focus on including older fish of known age.

2.4. Age structure and longevity

There is considerable evidence that Paddlefish can reach relatively old ages, but the longevity varies significantly among the stocks. Longevity of Paddlefish in each system will be affected by natural and fishing mortality, with low mortality rates necessary for systems with high longevity. The shortest life span was reported for the most southern stocks, such as Lake Pontchartrain, Lake Henderson and Atchafalaya River in Louisiana, where the oldest animals were reported to be 9 to 14 years old (Reed, 1992). Although the Alabama River is not a part of the Mississippi River drainage (it is a part of the Mobile Bay basin), it is worth noting that Paddlefish inhabiting this river and its tributaries exhibited an age structure similar to Louisiana stocks. For example, the oldest fish observed in the lower Alabama River in 1994 -1995 by Hoxmeier and DeVries (1997) and Lein and DeVries (1998) in Cahaba and Tallapoosa rivers in 1992-1995 were 11 years old. In the early 1980s, increased fishing effort resulted in a severe decline in Paddlefish abundance and size in the Alabama River. As a result, the Alabama Division of Wildlife and Freshwater Fisheries (ADWFF) placed a moratorium on the capture and possession of Paddlefish in Alabama waters in 1988. Rider et al. (2011) collected 201 fish from the same population in 2006, 18 years after the fishery closure, and estimated the oldest age in the sample to be 15 years for females and 17 years for males. Thus in the absence of fishing, some Paddlefish in the Alabama River survive at least up to age 17. Considering the relatively small sample size in this study, it is conceivable that older fish could have been present in the population.

The oldest fish have been reported from the northernmost edge of Paddlefish distribution. The maximum reported ages for Paddlefish in these areas range from 23 to 55 years (Purkett, 1963; Robinson, 1966; Rosen et al., 1982; Scarnecchia et al., 1996a, 2008, 2011; Runstrom et al., 2001). Most of the observations of the oldest fish were consistently made in the Missouri River basin. Rosen et al. (1992) reported the oldest age of 26 years from the collection of Paddlefish below Gavins Point Dam on the Missouri River in South Dakota – Nebraska. Pierce et al. (2011) reported a maximum age of 34 years for males and 43 years for females in Lake Francis Case, a reservoir on the Missouri River in South Dakota. The oldest fish that have been aged were observed farther north, in Lake Sakakawea,

a reservoir on the Missouri River in North Dakota, and the Yellowstone River in Montana; fish over 40 and 50 years old respectively, with a maximum age of 55 years, were noted repeatedly during the regular annual sampling of the recreational fishery, which targets the Paddlefish spawning run (Scarnecchia et al., 1996b, 2008, 2011). Although existing age validation studies (Scarnecchia et al., 2006) provide only partial evidence of appropriate age determination using dental bones (because they compared ages to times at large of tagged individuals), negative bias (under-ageing of older fish) was shown in some cases (Pierce et al., 2011), which may indicate that Paddlefish can live longer than 55 years. However, the overall evidence that Paddlefish can exceed ages of 40 - 50 years seems to be strong.

The maximum Paddlefish ages reported for the stocks located in the middle range of species' distribution (Illinois, Iowa, Kentucky, Missouri, Arkansas and Oklahoma) appear to be considerably less than those of the Missouri River (Missouri, North Dakota, South Dakota), but greater than those for the southern stocks in Louisiana, Mississippi and Alabama. The Paddlefish of Kentucky Lake are among the most studied populations in the central region, where the reported maximum age ranged from 11 to 21 years (Bronte and Johnson, 1985; Hoffnagle and Timmons, 1989; Timmons and Hughbanks, 2000; Scholten and Bettoli, 2005). However, Bronte and Johnson (1985) reported a maximum age of only 12 years for nearby Lake Barkley, Tennessee. Leone et al. (2011) found a maximum age of 16 years from three impoundments of the Arkansas River in Arkansas. A maximum age of 27 years was reported for Grand Lake, Oklahoma, a reservoir on the Arkansas River, by Scarnecchia et al. (2011), but it was argued that average life expectancy should be no longer than 20 years. Genderke (1978) estimated the oldest fish in the upper Mississippi River (Iowa) at 18 years, while Risely (2012) reported fish in the lower Mississippi River as old as 24 years. It is important to note that nearly all stocks in the central range have experienced periods of moderate and heavy exploitation, which clearly has truncated the age distribution having a significant negative effect on the maximum observed age. For example, maximum ages of 25 to 30 years were common in lightly exploited Paddlefish fisheries in the Osage River and the Lake of Ozarks (Purkett 1963). Potential underestimation of maximum age of Paddlefish in the central region is supported by low values of natural mortality estimated in the region, which were found to be in a range of 0.05-0.09 (Boone and Timmons, 1995; Timmons and Hughbanks, 2000; Donabauer et al., 2009). Such low natural mortality values suggest a substantially higher potential for the maximum age, at least 30 years and perhaps

greater than 50 years, when the relationship between maximum age and natural mortality is applied based on Sekharan (1975), Hoenig (1983), Hewitt and Hoenig, (2005).

Among all regions, the maximum age data for northern stocks (Yellowstone River, Sakakawea Lake, Lake Francis, Missouri River) seems to be well established. The maximum longevity for the northern stock appears to be in the range of 50 to 60 years. The maximum observed age in general declines from north to south with the lowest maximum age of 9 to11 years reported for Louisiana stocks (Reed et al., 1992). However, the maximum longevity of stocks in the middle range is not as clear. The moderate age structure of Paddlefish stocks in the center of their distribution is likely to be the result of fishery exploitation, thus the maximum longevity is likely to be underestimated. This is also likely true for the southernmost portion of the range. Low estimates of natural mortality suggest much higher longevity, similar to that observed for the northern stocks. Careful consideration of stock exploitation history has to be taken when maximum reported age is used to derive natural mortality rates for population analysis.

2.5. Growth

Paddlefish growth has received a great amount of attention throughout the Paddlefish's distribution. Earlier studies reported general range of size with some reference to specific ages (Stockard, 1907; Nichols, 1916, Adams, 1942; Houser and Bross, 1959; Purkett, 1963; Houser, 1965; Pasch et al., 1980). The use of the von Bertalanffy (1938) growth model gained ground in Paddlefish literature by 1980s, and most papers published in recent decades included von Bertalanffy (VB) parameters estimates (Rosen et al.,1982; Bronte and Johnson, 1985; Hoffnagle and Timmons, 1989; Reed, 1992; Lein and DeVries, 1998, Scholten and Bettoli, 2005; Leone et al., 2011; Scarnecchia et al., 2011 and others). However, despite the large number of published studies on age and growth, nearly all of them were stock or site specific. There is a clear need to review and synthesize available information for the entire Paddlefish range.

We approached the review and analysis of growth data in three different ways. We reviewed available published studies with respect to differences by sex, region, habitat type and developed summaries of growth parameters estimates. The second approach was to obtain representative data sets, preferably covering stocks from different geographic regions, different ecotopes with the sex specific information, to estimate growth parameters independently and test for differences whenever

possible. It is worth noting that the all published studies rely exclusively on age information inferred from age registering structures (mostly dentary bones) and thus are dependent on the quality of age determination. Low precision and bias in age readings, especially for older fish, may substantially affect parameters estimation and result in misinterpretation of population dynamics. The ageing error issue can be completely avoided when the tagging information is available. This opportunity was provided due to the existence of the Mississippi Interstate Cooperative Resources Agreement (MICRA) tagging database which consolidates all tagging information on the release and recapture of Paddlefish by member states of MICRA. These data were analyzed by basin as well as by river systems.

The original raw data made available for this study included individual data on age, size (eye to fork length or EFL), weight and sex for the following systems: Kentucky Lake, data collected by Scholten and Bettoli in 2003 and 2004 (Scholten and Bettoli, 2005), three impoundments of Arkansas River Lake Dardanelle, Lake Ozark and Pool 13 (described in Leone et al, 2011), Lower Mississippi River data collected by Tripp et al. (2012) and data for all states combined extracted from MICRA tagging database.

Size frequency histograms by age were plotted for each dataset (Figures 2.5.1-2.5.4) and reviewed for symmetry and normality of distribution with QQ plots. Variability of data was summarized by boxplots at age (Figures 2.5.5 -2.5.8). Mean size at age (EFL, cm), standard deviation (SD) and coefficient of variation (SD/mean; CV) were calculated to characterize variability at size for further use in modeling the exploitation pattern based on size distribution at age. CVs of size at age were nearly constant for all age groups at 5-6% (Tables 2.5.1.- 2.5.4), while the average CV estimated from known age fish in the MICRA tagging data was 12%, indicating a wider spread of size at age.

The VB growth function was fit to the available data sets with age and size data:

$$L_{(t)} = L_{\infty}(1 - e^{-K(t-t_0)}),$$

where L_{∞} is the theoretic maximum length, K is the Brody growth coefficient, t_0 is the predicted age at which length is zero and t is time in years.   These parameters were estimated using the nonlinear regression procedure in R statistical software (R-project, 2013). Differences among growth curves fitted to the original data were tested using analysis of residual sum of squares (ARSS, Chen et al., 1992) and likelihood ratio tests (Cerrato, 1990).

A family of VB growth curves based on estimated and published parameters is shown on Figure 2.5.9. Corresponding VB parameters are presented in Table 2.5.5.   The wide spread of

asymptotic maximum length L_∞ as well as variable steepness (slope) of curves at the origin indicates significant variability of Paddlefish growth. Large differences in the growth of Paddlefish, especially early growth, was also reported in earlier studies. Growth variability is thought to be due to gender maturation differences, geographic location in latitudinal aspect (defines length of growth period), and food availability (productivity of the water body).

Separating VB growth curves by sex appears to substantially reduce the variability (Figures 2.5.10 and 2.5.11), suggesting that there is indeed a difference in growth between the sexes. Many studies suggested a presence of sex specific differences in growth rates and maximum size attained, while others did not find any differences. Rosen (1976) and Rosen et al. (1982) found sexual dimorphism in Paddlefish where females had greater length and weight than males at any age. Hoyt (1984) found males to be larger through age 5, after which females were larger. Faster growth and larger maximum size of females was also reported for Yellowstone-Sakakawea stock of Paddlefish in eastern Montana and western North Dakota (Scarnecchia et al., 2008), Grand Lake, Oklahoma (Scarnecchia et al., 2011) and three impoundments of Arkansas River, Arkansas (Leone et al. 2011).

At the same time, Alexander et al. (1987) found no sexual dimorphism until maturity at age 8 and about 1,000 mm, when females became heavier than males at any length. Bronte and Johnson (1985) and Hoffnagle and Timmons (1989) did not find any growth specific differences among sexes for Kentucky Lake and Lake Barkley. Reed (1992) detected no differences in growth between males and females for three stocks in Louisiana. Hoxmeier and DeVries (1997) found that growth rates did not differ between sexes or among habitats in Alabama River. However, very few studies subjected comparison of growth rates to formal statistical analysis with the exception of Rosen et al. (1982), Hoxmeier and DeVries (1997), and Leone et al. (2011).

We tested the growth data for Lake Dardanelle, Lake Ozark and Pool 13 using likelihood ratio tests and reconfirmed the conclusions by Leone et al. (2011) on differences in growth between males and females. We also found a significant difference (likelihood ratio test, P <0.0001) between growth of males and females for Kentucky Lake using the Scholten and Bettoli (2005) data. Differences in growth between males and females were also found to be highly significant (likelihood ratio test, P << 10^{-6} for L_∞ and K) in the recent study of Paddlefish in Lower Mississippi River (J. Risley, personal communication). Thus, effectively all data sets that were available to us confirmed sex specific differences, with females generally growing faster and attaining larger maximum size. Pair-wise

comparison of reported (but not tested for differences) sex-specific growth curves generally confirms our results (Figures 2.5.12- 2.5.26).

Previous studies indicated that growth of Paddlefish seems to be directly related to the length of the growing season and food abundance. For example, Hageman et al. (1986) reported that length, weight, and age information gathered on the Paddlefish population in Lake Cumberland indicated that the species grows faster, reaches sexual maturity sooner, and has a faster recruitment potential than similar populations in most large rivers. Hoxmeier and DeVries (1997) found that Paddlefish in channel habitats were significantly larger than those in both oxbow and backwater habitats (ANOVA, $P = 0.0001$). In addition, length-frequency distributions differed among habitats where oxbow lakes contained relatively more, smaller fish, and the channel habitat contained relatively more, larger fish. Growth of Paddlefish in reservoirs and river-lakes (e.g., Lake Pepin in the upper Mississippi River) was reported to be faster than in riverine habitats, likely reflecting higher food abundance and availability (Stockard, 1907; Rosen, 1976; Russell, 1986). Reed et al. (1992) suggested that differences in Paddlefish growth between populations can probably be explained by differences in latitude and habitat with Paddlefish growing faster at southern latitudes owing to a longer growing season. Paukert and Fisher (2001) reported that Paddlefish in lentic habitats had greater mean length at age than Paddlefish in lotic habitats, as previously found by Lein and DeVries (1998). Similarly, Leone et al. (2011) compared three impoundments of Arkansas River and reported that Paddlefish from the most lentic pool, Lake Dardanelle, had the highest growth rate and had the highest mean condition factor, weight, and fecundity. In contrast, Paddlefish from the most lotic impoundment, Pool 13, had the slowest growth, and the lowest mean condition, weight, and fecundity.

Although we could not test for the differences among published estimates using formal statistical techniques due to lack of access to the majority of original data and no standard errors reported for K and L_∞ in published papers, the summary of estimates of K and L_∞ (Table 2.5.5) clearly indicate differences among regions and among stocks within regions.

We used data from the MICRA Paddlefish tagging database to estimate growth patterns using two modeling approaches: age-based, and increment based. Sexes were combined because not enough sex-specific data were available to conduct sex-specific analyses. All lengths were EFL, and all of the analyses assigned the location based on the recovery site rather than the release site, which allows direct comparisons with other growth studies that captured individuals in specific locations.

Age-based VB growth models were applied to known age fish from stocking activities and fish that had been aged from the MICRA tagging database and from several other sources. We developed a hierarchical von Bertalanffy growth model with random effects for each of the parameters (He and Bence 2007). The hierarchical model estimated overall mean parameters, deviations from the mean for each basin (Gulf, Mississippi, Missouri, Ohio), and deviations within each basin for each reach. The overall model is the traditional age-based VB growth model,

$$\hat{L}_{i,a,r} = L_{\infty,r}\left(1 - e^{-K_r(a_i - t_{0,r})}\right),$$

where $\hat{L}_{i,a,r}$ is the estimated length of individual i at age a in reach r, $L_{\infty,r}$ was the asymptotic average maximum length in each reach, K_r was the growth coefficient for each reach, and $t_{0,r}$ was the theoretical age at size zero in each reach. The parameters for each reach were estimated as the sum of the grand average and deviations for basin and reach,

$$L_{\infty,r} = L_{\infty} + \delta_r,$$

$$K_r = K + \varepsilon_b + \varepsilon_r,$$

$$t_{0,r} = t_0 + \epsilon_b + \epsilon_r,$$

$$\delta_r \sim N\left(0, \sigma_{\delta_r}^2\right), \varepsilon_b \sim N\left(0, \sigma_{\varepsilon_b}^2\right), \varepsilon_r \sim N\left(0, \sigma_{\varepsilon_r}^2\right), \epsilon_b \sim N\left(0, \sigma_{\epsilon_b}^2\right), \epsilon_r \sim N\left(0, \sigma_{\epsilon_r}^2\right),$$

where L_{∞} was the grand average for asymptotic average length, δ_r was the deviations in L_{∞} for each reach, K was the grand average growth coefficient, ε_b and ε_r were the deviations in K for each basin and reach, t_0 was the grand average age at size zero, ϵ_b and ϵ_r were the deviations in t_0 for each basin and reach, and the σ^2 terms were the variances for each random effect. Reaches were nested within basins. All of the random effects were assumed to be normally distributed. We estimated the parameters of the model using a maximum likelihood approach in AD Model Builder (Fournier et al. 2012) assuming normally distributed errors in length at age. We did not include a basin effect for L_{∞} because a preliminary model estimated the variance for that set of parameters was zero.

Parameters of the growth curves differed substantially among reaches and basins (Tables 2.5.6 and 2.5.7). Most of the variability was at the reach level for asymptotic length, but K and t_0 showed substantial variation at the basin level (although the SEs were quite large). On average, the Paddlefish in the Gulf basin had the fastest growth, followed by the Ohio and Mississippi basins (Figure. 2.5.27). Paddlefish in the Missouri basin grew the slowest of the four basins. Substantial variation also existed at the reach level with the fastest growth occurring in the Red River-Lake Texoma and Allegheny River - Kinzua Holston - Cherokee reaches and the slowest growth occurring in the two reaches in the

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Missouri basin, Below Gavins Point Dam and Fort Randall Dam Tailwaters. Because ages from readers were used for several reaches in the analysis (Lake Dardanelle, Lake of the Ozarks, Pool 13 and Kentucky Lake), error in age estimation could affect parameter estimates. However, aging error should have a minimal effect on estimated mean length at age in the other reaches.

Increment-based approaches were applied to recaptured fish when initial length, length at recapture, and time at large data were available. We developed a hierarchical VB growth model with random effects for each of the parameters (Hart and Chute, 2009). The model included reach and basin level variability in L_∞ and basin level variability in K. Parameters from more complex models were not estimable. The increment von Bertalanffy model estimates the change in length based on the length at initial capture and the time at large,

$$\widehat{\Delta L}_{i,r} = (L_{\infty,r} - L_{i,r})(1 - e^{-K_r \Delta t_i}),$$

$$L_{\infty,r} = L_\infty + \delta_b + \delta_r,$$

$$K_r = K + \varepsilon_b,$$

$$\delta_b \sim N(0, \sigma_{\delta_b}^2), \delta_r \sim N(0, \sigma_{\delta_r}^2), \varepsilon_b \sim N(0, \sigma_{\varepsilon_b}^2),$$

where $\widehat{\Delta L}_{i,r}$ was the estimated growth increment for individual i in reach r, $L_{i,r}$ was the length at release, and Δt_i was the time at large. The definitions of the other parameters are the same as for the age-structured model. Reaches were nested within basins. A benefit of this model is that ages of the individuals are not needed to estimate the growth parameters.

We estimated the parameters of the model using a maximum likelihood approach in AD Model Builder (Fournier et al. 2012) assuming normally distributed errors in the growth increment. The model was not able to estimate reach level effects for both L_∞ and K. Therefore, we fitted models with basin effects for one parameter and reach effects for the other and chose the model with the lowest negative log likelihood (reach effects for L_∞ and basin effects for K). The difference in the negative log likelihood was 11.1 log likelihood units.

The results of the increment model were similar to those from the age-based model, with the most rapid growth occurring in the Gulf basin and the slowest in the Missouri basin (Table 2.5.8). The largest asymptotic size was estimated for the Allegheny-Kinzua reach and the smallest was for the Wabash River.

We expect some difference in the results of the length-based and increment based models because their error structures are different. The age-based model assumes that differences in

individual fish lengths from the mean length at age for a reach are normally distributed. In contrast, the increment model assumes that differences between the observed and mean growth increments are normally distributed. This difference in error structure can lead to differences in predicted size at age. There is not general agreement on which approach is better, but the age-based approach provides the estimates necessary for the length-based mortality estimation (described below).

We assumed that growth patterns were constant over time within a reach. The data simply were not available (i.e., there were not enough records) to attempt to estimate time-varying growth patterns. Additionally, some simplifications of the overall hierarchical model, such as removing random effects for basin or site, were necessary because of the limited number of observations for many of the reaches or limited number of reaches within a basin.

2.6. Length-weight

Length and weight of individual fish are some of the easiest and most frequent measurements that are recorded and for this reason length - weight relationships have been described abundantly for Paddlefish (Genderke, 1978; Combs,1982; Rosen et al., 1982; Bronte and Johnson, 1985; Hageman et al. 1986; Reed et al. 1992; Scholten and Bettoli 2005; Scarnecchia et al., 2008; Scarnecchia and Gordon, 2011; Leone et al., 2011; Risely, 2012; Tripp et al., 2012). The relationship between total length (L) and total weight (W) for all Paddlefish stocks isdescribed by standard equation:

$$W = aL^b$$

Parameters a and b usually have been estimated using linear regression after a logarithmic transformation (either normal base *e* or base 10) with a slope of b and intercept log*a*:

$$\log W = \log a + b \log L$$

The summary of published parameters and estimated in this study is presented in Table 2.6.1. These parameters were used to derive stock specific weights at age in Paddlefish population analysis. In a few cases when we had an opportunity to re-estimate length weight relationship using raw data, we used those estimates over the published ones.

There is substantial variability in relationship between length and weight for Paddlefish (a general characteristic of all fish species) due to the individual differences in condition (robustness) of individual fish (see the spread on individual data points around the fitted curve, Figures 2.6.1 – 2.6.14). Condition reflects food availability and individual growth history. The average condition of each population varies seasonally and yearly and may affect comparisons among and within

populations depending on timing of sampling. Sex and gonad development are other important variables. Nearly all data sets that we tested (ANCOVA) indicated significant or highly significant differences in weight at age between males and females. These differences were shown for Paddlefish of Kentucky Lake, Arkansas River (pooled data), Missouri, Mississippi, Ohio and Gulf basins (MICRA tagging database data).

There are clearly differences in weight attained at the same size among stocks within river systems or regions (Figure 2.6.15). There are two significant outliers on Figure 2.6.15: Lake Barkley males and Kentucky Lake females, both reported in Bronte and Johnson (1985). We suspect that there might be a calculation or reporting error and use of these particular set of parameters would require additional verification. Elimination of these outliers results in relatively tight family of length-weight curves that represent variability in weight at size (Figure 2.6.16). We could not re-test published parameters beyond common sense errors, but MICRA tagging data set provides an opportunity for comparing length-weight relationships at various levels of detail (basin, river system, lake or pool). We provide here a comparison of length weight by basin, as defined in database: Mississippi, Missouri, Ohio, and Gulf (Figure 2.6.17). Figure 2.6.17 shows that the Paddlefish in Mississippi basin appear to have the largest weight at length, while the Paddlefish in Missouri attain the lowest weight at the same length, whith fish from Ohio and Gulf basin in the middle of the two extremes.

Status of knowledge of length weight relationship.

There is sufficient information accumulated on length-weight relationships for appropriate quantitative description throughout the distribution. Overall evidence suggests presence of sex- and region-specific differences that may be caused by sex specific life history traits and variability in aquatic ecosystems productivity. These differences are likely to have significant effect on individual weight at age, total biomass production and population fecundity and should be accounted for in the calculation of reference points.

2.7. Maturity

Paddlefish require several years of growth before they become sexually mature and often are characterized as late maturing (Jennings and Zigler, 2000). The age and size of first maturation varies by region and type of water body (riverine or lacustrine), likely reflecting local growth conditions (Jennings and Zigler, 2000, Table 2.7.1). Males generally mature earlier than females (Jennings and Zigler, 2000). Throughout most of their range, the age of first maturation for males is rather consistent at 5 to 6 years of age. Males begin to mature at age 5 or 6 in Kentucky Lake (Hoffnagle and Timmons, 1989), the Tennessee and Cumberland Rivers (Timmons and Hughbanks, 2000), Grand Lake (Scharnechia et al., 2011), Lake Barkley (Bronte and Johnson, 1985), Lake Cumberland (Hageman et al., 1986), the Arkansas River (Leone et al., 2011), the Atchafalaya River and Lake Pontchartrain (Reed et al., 1992), and the Alabama River (Lein and DeVries, 1998). The youngest age of male maturation (age 4) was reported for Kentucky Lake (Scholten and Bettoli, 2005) and the upper Mississippi River (Gengerke, 1978). A substantially longer time is required for males to become mature in the most northern range of distribution, including South Dakota, North Dakota, and Montana. Males begin to mature at age 8 in the Missouri River below Gavins Point Dam (Rosen et al., 1982) and Lake Francis Case, South Dakota (Pierce et al., 2011). Slow growth is thought to be responsible for late male maturation at ages 9-15 in Lake Sakakawea and the Yellowstone River (Scarnecchia et al., 2008). Full maturation of males occurs within 2 to 6 years from the first age of maturity (Table 2.7.1).

Female Paddlefish begin to mature at 5-6 years old in southern areas such as the Atchafalaya River and Lake Pontchartrain (Reed, 1992), while females in the Arkansas River were reported to begin to mature as early as age 7 (Leone et al., 2011). Age of first maturity in the central region, where the majority of observations were made, is between 8 and 10 years. This includes Kentucky Lake (Hoffnagle and Timmons, 1989; Scholten and Bettoli, 2005), the Tennessee and Cumberland Rivers (Timmons and Hughbanks, 2000), Grand Lake (Scharnechia et al., 2011), Lake Barkley (Bronte and Johnson, 1985), Lake Cumberland (Hageman et al., 1986), and the Missouri River below Gavins Point Dam. As with males, females in the most northern region begin to mature late, at age 11 in Lake Francis Case (Pierce et al., 2011) and 14-15 in the Yellowstone River and Lake Sakakawea (Scarnecchia et al., 2008). The percentage of sexually mature individuals in each year-class increases until 100% are sexually mature (Timmons and Hughbanks, 2000).

Spawning frequency

There is a prevailing theory that Paddlefish, particularly females, do not spawn on an annual basis, but rather have an inter-spawning interval of 2 to 3 years or even more, depending on latitude and water-body productivity (Carlson and. Bonislawsky, 1981). For example, Jennings and Zigler (2000) stated that *"Male Paddlefish are able to spawn each year, but several studies suggest female Paddlefish may require 2 to 5 years to develop mature ova."* Their statement relies mostly on a study by Meyer (1960), who concluded that female Paddlefish spawn every 4 to 7 years based on the analyses of annuli spacing on Paddlefish dentary bones. Similarly, Scarnecchia et al. (1989) indicated that *"Female Paddlefish do not spawn every year and evidently spawn only every 2-3 years in Missouri (Russell 1986) and every 4- 7 years in Iowa (Meyer 1960)".* However, they admit that " *These conclusions were based on the spacing of annuli on dentary bones, and the exact periodicity of Paddlefish spawning is not known.*" Russell (1986) suggested that female Paddlefish in Missouri may make spawning runs only every 2 to 3 years because maturation of the oocytes requires a minimum of 2 years. Runstrom et al. (2001) used this observation as an explanation of intermittent recruitment success being characteristic of Paddlefish life history.

Many studies have shown that adult females sampled during and after the spring spawning season frequently contain ovaries with immature eggs (Alexander and Peterson, 1982; Rosen et al., 1982; Hageman et al., 1986; Leone et al., 2011). Hageman et al. (1986) noted that *"Sexually mature, non-gravid females occurred in the lake portion of Lake Cumberland while only mature, gravid females concentrated in the upper tributaries of the lake during the spawning season lent credence to the theory proposed by Houser and Bross (1959), Meyer (1960), and Carlson and Bonislawsky (1981) that mature female Paddlefish do not spawn every year, but do so on an alternate year basis."* It appears that in discussing spawning frequency, most papers rely on a limited number of studies that present only circumstantial evidence (Meyer, 1960; Russell, 1986). No studies have been presented yet that clearly demonstrate skip-spawning. The strongest evidence so far seems to be observations made prior to and during spawning in different regions, showing that non-gravid females of the size and age similar to gravid females are a substantial fraction of the total number of observed females (Rosen et al., 1982; Scholten and Bettoli, 2005; Leone et al., 2011).

The initial reasoning to explain the skip-spawning phenomena in Paddlefish was provided by Houser and Bross (1959), based on the analogy with sturgeon species. Russell (1986) suggested that

the long interval between spawnings may result from the need to acquire and mobilize the energy required to produce the large egg masses of female Paddlefish, which can comprise up to 25% of the body weight (Purkett, 1963). This is also suggested by Scarnecchia et al. (1989), who stated *"It may thus be several years after maturity before a given female is physiologically prepared and receives the appropriate environmental stimuli to initiate spawning."*

As suggested in Russell (1986), Scarnecchia et al. (2011), and others, the frequency of individual female spawning is likely dependent on its ability to accumulate energy and store fat, and thus is dependent on the productivity of the system and the length of the growing season. This in turn suggests that the frequency of spawning is likely to vary individually and among the populations, which will have a direct effect on the percent of gravid females in the population each spawning season. Lallaman (2012) concurred with this by stating *"Female spawning periodicity also ranges from 1-2 years in the south, compared to 2-5 years in the north (Jennings and Zigler 2000). This variability in reproductive strategy makes assessing sex and spawning condition a challenge, as the proportion of spawning adults and sex ratio may differ within and between populations."*

There are very few studies that report observations on percent gravid females in pre-spawning or actively-spawning populations of Paddlefish. Scholten and Bettoli (2005) reported a maximum of 82% maturity at age 10 for females in Kentucky Lake. They noted that there was no age-class of either sex in which all of the individuals were mature, but all females (*n* = 21) equal to or longer than 1,034 mm entire fish length (EFL) were mature. Leone et al. (2011) also reported an increase in the percent of gravid females from 8% at age 7 to 78% (range = 67–100%) for ages 14–16 fish in three impoundments of the Arkansas River. Risely (2012) reported that female Paddlefish in the lower Mississippi River were first maturing at age 10 with 24% of gravid females in this age class. Thirty-eight percent of fish of ages 12-19 were gravid and 100% of fish of ages 20-24 were gravid (Risely (2012). If 100% of the fish are gravid for a range of sizes or ages, this suggests that they will all spawn that year. If females spawn every 2-3 years, we would expect only 33-50% to be gravid in any given year.

Standing apart from all of the above stocks is the Grand Lake Paddlefish population on the Arkansas River in Oklahoma. Data collected by the Oklahoma   Department of Wildlife Conservation indicated a knife-edge type of maturity with the percent of gravid fish jumping from 0% at age 7 to 95% at age 8 and 100% age 9 and older (Scarnecchia et al., 2011). However, it is important to note that nearly all of the Paddlefish subjected to maturity examinations were collected from the sport-

snagging fishery during spawning migrations. This certainly is likely to bias the percent gravidity estimates, as well as estimates for the frequency of spawning. If non-gravid mature females remain in the main body of the reservoir and do not participate in the spawning migration upstream, the percent gravidity for the population is likely to be overestimated. However, some unpublished data suggest that the overall proportion of gravid females harvested in the Grand Lake is also very high (98%), although lower than that in the riverine section (99.5%, Jason Schooley, personal communication). Data collected by the Oklahoma Department of Wildlife Conservation strongly suggest a fast maturation and regular annual spawning of Paddlefish in Grand Lake, which is in contrast with traditional paradigm of skip-spawning.

Maturity schedule

Maturity schedules for Paddlefish (maturation progress with age) have not been presented much in the literature. Some data were reported either in tabular form or as a summary for Kentucky Lake by Timmons and Hughbanks (2000) and Scholten and Bettoli (2005), impoundments of the Arkansas River (Leone et al., 2011), and the lower Mississippi River (Risely, 2012). However, relationships of maturity-at-age or maturity-at-size have generally not been estimated..

We developed estimates of maturity–at-age for several stocks using published data or data provided to us by state biologists. Data on maturity-at-age and maturity-at-size were fit by a logistic function,

For age:

$$P = \frac{m}{1 + e^{-k(age-\gamma)}}$$

For size:

$$P = \frac{m}{1 + e^{-k(lengh-\gamma)}}$$

where P is proportion of gravid females, m is the maximum percent of gravid females, k is the rate of increase in maturity and γ is the age or size at 50% maturity (Quinn and Deriso, 1999).

In most cases, a logistic function was fit to the maturity-at-size data, then maturity-at-age was calculated by applying mean size at each age estimated from the VB growth function. The principal

reasons for using maturity and size during the first step were either the lack of aging data or the small number of age groups for which data on gravid females were available. In addition, it seems reasonable to assume that maturation is likely to be related mostly to size (a female needs to grow to a certain size to be able to accumulate sufficient energy to begin producing eggs), rather than age (there is large size variability at age), although both variables are obviously correlated. A reliable estimate of maturity curve requires a random sample of individuals from the population. Violations of this requirement will cause biased estimates of the maturity curves.

Arkansas River

Data for three impoundments in the Arkansas River (Lake Dardanelle, Ozark Lake, and Pool 13) were provided in annual monitoring reports of the Arkansas Game and Fish Commission covering the period from 2003 to 2012 (Leone et al., 2004; Leone et al., 2006; Quinn et al., 2006; Leone et al., 2009; Leone et al., 2010; Leone et al., 2011; Leone and Quinn, 2012). Since the annual sample size for individual pools and years were relatively small, data on maturity for all pools and years were combined to produce a single maturity curve (Table 2.7.2). Percent gravidity of Paddlefish females in the Arkansas River rises from near 0 at 34 inches EFL to a maximum of 76% at 39 inches EFL and larger (Figure 2.7.1, Table 2.7.2). These results suggest that some female Paddlefish in Lake Dardanelle, Ozark Lake, and Pool 13 do not spawn on an annual basis upon reaching maturity. If 50% of females spawned each year and 50% spawned every other year, we would expect to find 75% gravid females, which is very close to the estimates for the Arkansas River. Maximum percent gravidity is achieved approximately at age 14 or an EFL of 40 inches (Figure 2.7.2). If growth differences are taken into consideration, females in Lake Dardanelle would reach full maturity by age 13, while females in Ozark Lake and Pool 13 will only reach by age 17 due to slower growth.

Kentucky Lake, Tennessee.

Data for Kentucky Lake were collected by Scholten and Bettoli (2005) in 2003 and 2004 in lacustrine and riverine sections of the lake using gillnets before (fall) and after (spring) the commercial fishing season. A summary on the number of collected gravid and non-gravid females is presented in Table 2.7.3. Scholten and Bettoli (2005) noted that "*There was no age-class of either sex in which all of the individuals were mature, but at least 50% of the age-5 males and age-10 females were mature. One age-11 female was not mature; however, all females (n = 21) equal to or longer than 1,034 mm*

EFL were mature." When all three parameters were freely estimated, the fit resulted in asymptotic maturity (parameter m) slightly larger than 1 (Figure 2.7.3, Table 2.7.8), although all parameter estimates were highly significant. As an alternative, we elected to fix m at 1 and re-estimate k and γ, thus forcing the curve to 100% maturity at EFL greater than or equal to 43 inches. However, the resultant curves and parameter estimates were very similar (Figure 2.7.4, Table 2.7.8). This corresponds to 100% maturity being achieved at approximately age 20 years (Figure 2.7.5).

Grand Lake, Arkansas River, Oklahoma.

Data on Grand Lake, Oklahoma were kindly provided by Jason Schooley, Oklahoma Department of Wildlife Conservation. A summary of the number of collected gravid and nongravid females by size and age is presented in Tables 2.7.4 and 2.7.5. These represent 6,361 female Paddlefish collected during 2008-2011. A free-parameter fit to the model resulted in an asymptotic maturity estimate of 93% (Figure 2.7.6, Table 2.7.8), although empirical data indicated that fish of size 36 inches EFL and larger are 100% mature (Figure 2.7.6) When asymptotic maturity was fixed at m=1, the curve appeared to better fit full range of empirical data (Figure 2.7.7). The maturity schedule for Paddlefish females in Grand Lake appears to be unique in the sense that the interval between the beginning of maturation and full maturity is very short, both in terms of size (30 to 36 inches) and age (8 to 9 years, Figure 2.7.8). Such knife-edged maturation appears to be rather unusual.

Lower Mississippi River, Arkansas.

Maturity data on female Paddlefish in the lower Mississippi River, Arkansas were collected during the 2008-2009, 2009-2010, and 2010- 2011 commercial seasons by the staff of the Arkansas Game and Fish Commission (AGFC) Fisheries Division. Data used in this analysis include those kindly provided by Jeremy Risley (AGFC) and those reported in Risley (2012). A summary of the number of collected gravid and non-gravid females by size and age is presented in Tables 2.7.6 and 2.7.7. The fit of the logistic curve to the data presented a challenge, due to the low sample size and apparent variability in maturation rate. While the total number of examined female was 267, the number of mature females was only 60, and when allocated by size or age classes, there were only single numbers of mature females observed in many size or age classes.

Free-fit of the logistic curve to the size at maturity data produced an estimate of asymptotic maturity of m= 0.46 (Figure 2.7.9, Table 2.7.8), which is a low estimate in our opinion. However, the

model would fail to fit when m was fixed at 1. When size intervals were increased to two inches, the model was fit with an estimate of m= 0.73 (Figure 2.7.10, Table 2.7.8). This would suggest a 73% maximum gravidity, a value similar to that estimated for the Arkansas River. However, this level of maturity will be achieved only when fish grow to the size of 45 inches (114.3 cm), while the asymptotic maximum length of the VB growth equation L_∞ for this stock was estimated at 42.6 inches (108.3 cm). Therefore, the actual percent gravidity in the population would never reach an asymptotic value of 73%

The fit to the age data resulted in value of m well above 1 (m= 1.63) and a poor fit (Figure 2.7.11). When m was fixed at 1, the model fit the data, but the curve approximates 100% gravidity only by age 30.

Given the difficulty of the model fit to the full range of data due to the sample size and variability, and also given the fact that the model fitted the maturity-at-size with 2 inch interval rather well, we considered that fit to the size data based on the 2 inch size intervals to be the most appropriate for the lower Mississippi River stock. The summary of all estimated maturity schedules by stock as a function of size and age is presented in Table 2.7.9 and Figure 2.7.12.

2.8. Fecundity

Paddlefish are rather fecund and a large female can produce over half a million eggs (Lein and Devires, 1998; Scholten and Bettoli, 2005). Average egg diameter is reported to range from 2 to 3.4 mm (Table 2.8.1, Hageman et al., 1986; Rosen et al., 1982; Reed et al., 1992; Lein and DeVries, 1998; Scholten and Bettoli 2005; Rider et al., 2011). The variability of egg size within an ovary is rather similar to that reported among the fish in the population. Hageman et al. (1986) reported an increase in egg diameter from 2.0 mm in October to 3.0 mm in April following an eggs maturation. Similar observations were reported by Lein and Devries (1998). Scholten and Bettoli (2005) noted a weak positive relationship between mean egg diameter and body weight ($P = 0.01$; $r^2 = 0.15$), but not EFL ($P = 0.34$; $r^2 = 0.01$).

Paddlefish ovaries were reported to vary in weight between 0.75 kg to nearly 5 kg (Table 2.8.1) and weigh up to 25% of female body weight (Purkett, 1961). However there is very large variation in individual fecundity of fish of similar size as well as variation by region (Figures 2.8.1 and 2.8.2; Russell, 1986; Reed et al., 1992; Lein and Devries, 1998; Scholten and Bettoli, 2005; Leone et al., 2011). Due to large variability in eggs per female, Hageman et al. (1986) went as far as concluding that "no correlation was observed between ova number and fish size".

Leone et al. (2011) reported that both absolute and relative fecundity varied inter-annually, at least in one impoundment (Pool 13) of Arkansas River. They also reported that fecundities for fish of similar lengths from Ozark Lake and Pool 13 fish were lower than those of fish in Lake Dardanelle (ANCOVA: $P < 0.001$). This is likely a reflection of the food availability or reservoir productivity, as fish from Lake Dardanelle exhibited the fastest rate of growth.

The relationship between fecundity and length or weight of the fish is available for several stocks (Table 2.8.2) and usually described as a linear function of the number of ova versus length or weight (Genderke, 1978; Lein and DeVries, 1998; Risely, 2012). Alternatively, a log-log plot can be used to plot the number of ova versus length or weight (Reed et al., 1992; Scholten and Bettoli, 2005; Leone et al., 2012; Rider et al., 2011). Both length and weight are significant predictors of the number of eggs, but they explained relatively little variation (low r^2 values) in all studies except for Lein and Devries (1998; Table 2.8.2). However in most studies fecundity had stronger correlation with weight compared to length (Table 2.8.2). While there is large variation in fecundity at size (Figure 2.8.3) and weight (Figure 2.8.4) among stocks, relative fecundity seemed to be rather constant (Table 2.8.1,

Figure 2.8.5). Fish from Kentucky Lake, Arkansas River, Alabama River drainage seemed to have very similar relative fecundity between 15 and 16 thousand eggs per kg of body weight. The exception was Paddlefish from Lake Pontchartrain in Louisiana with much lower relative fecundity at 9.5 thousand eggs per kg body weight. Fecundity of Paddlefish in Lake Pontchartrain appeared to be less than fecundities reported for populations north of Louisiana (Upper Mississippi River, Kentucky, Arkansas, Lower Mississippi) as well as populations in Alabama located at similar latitudes. Smaller absolute fecundities of Louisiana female Paddlefish for which fecundities were estimated may reflect the relatively small size (mean weight 11.3 kg) of fish included in the sample. Additionally, lower weights and increased egg diameters result in reduced relative fecundity of Paddlefish in Louisiana in comparison to northern populations. Relative fecundity of Lower Mississippi River was on the higher end of the spectrum (18.8 thousand eggs/kg) and similar to that in the Alabama River (19.4 thousand eggs/kg; Lein and DeVries,1998).

Because we were not provided the raw data for any of the studies, except for those in the Arkansas River, we were unable to test for significant differences between fecundity–weight or fecundity-length relationships among stocks.

Summary of the status of knowledge on fecundity

Several studies provide a general overview of the range of Paddlefish fecundity. Information for several stocks is sufficient for use in population dynamics modeling (Arkansas River, Kentucky Lake, Lower Mississippi and Alabama Rivers). In some cases (Lake Sakakawea, Grand Lake) fecundity data appeared to be collected regularly but have not been summarized yet in reports or publications. Information on relative fecundity is somewhat conflicting. On one hand, reported relative fecundity seemed to be rather similar for a number of stocks. On another hand, slopes of regression line of absolute fecundity and weight appeared to be rather different. We recommend using stock specific fecundity whenever possible. In cases when no data are available, information can be borrowed from another stock with similar life history characteristics.

2.9. Natural Mortality

Natural mortality is one of the most important parameters in fisheries stock assessment and management. The magnitude of natural mortality directly affects the productivity of the stock, the yields that can be obtained, optimal exploitation rates, and biological reference points (Brodziak et al., 2011). Unfortunately, natural mortality is one of the most uncertain quantities. In the majority of stock assessments, natural mortality is not based on reliable data from the stock being assessed, but is chosen by experts, borrowed from other stocks or species, calculated from general empirical relationships, or based on life history theory. Natural mortality is also usually assumed to be constant over time, age, and sex, which may not to be true for many stocks.

There are several groups of methods to estimate natural mortality. These include methods that are based on mark-recapture data (e.g., Chapman, 1961; Seber, 1982), catch-at-age (e.g. Chapman and Robson, 1960; Paloheimo, 1980), maximum observed age (Hoenig, 1983), life history theory (Roff, 1984; Charnov, 1993; Jensen, 1996; Alverson and Carney, 1975), and empirical relationships (Pauly, 1980; Gunderson, 1997; Hoenig, 1983). Another group of methods is based on estimation of deaths due to predation (Gislason et al., 2010) and generally is used for forage species. Detailed reviews of various methods for natural mortality estimation can be found in Vetter (1988), Brodziak et al. (2011), and Kenchington (2013). Each of these methods has its benefits and deficiencies and there is no single generally accepted approach for selecting values for natural mortality used in fisheries stock assessment.

Past estimates of Paddlefish natural mortality

Estimation of Paddlefish natural mortality presents challenges and limitations similar to other species of fish. Relative to most stocks, however, there are many estimates of natural mortality in the literature.

Northern stocks (Montana, North Dakota, South Dakota, Nebraska)

Rosen et al. (1982) attempted to estimate total mortality and partition it into fishing and natural mortality components based on tag returns for the Paddlefish in the South Dakota–Nebraska section of the Missouri River. The results for the two best data sets were inconsistent. In 1972 total mortality was estimated at $Z = 0.40$ and natural mortality at $M = 0.35$, but in 1975 Z was estimated at 0.92 and M at

0.81. Because of the unresolved problems concerning the non-reporting of tags, as well as the apparent migration of tagged fish and immigration of untagged fish during the study, they questioned the reliability of these results. In addition to tagging, Rosen et al. (1982) produced a catch-curve analysis which yielded an instantaneous total mortality rate (Z) estimate of 0.20 or an annual total mortality of 18%, thus placing an upper limit for M at 0.2. However, Rosen et al. (1982) suggested that exploitation probably contributes to at least half the mortality, while natural mortality of adult Paddlefish may be quite low.

Runstrom et al. (2001) estimated the total mortality of a protected, unexploited population of Paddlefish in the Wisconsin River, a tributary of the upper Mississippi River, based on data collected in 1993 and 1994. The estimate of annual mortality derived from catch-curve analysis was 0.27. However the quality of the model fit was poor, the slope estimate was based on only four data points (ages 15 -18) with very small numbers of fish per age group. Runstrom et al. (2001) considered this estimate to be high and speculated that it may be attributed to emigration and error in age estimation.

Stocks in the center of distribution (MO, KY, AR, OK, TN)

Boone and Timmons (1995) estimated the annual natural mortality of Paddlefish to be less than 9% in South Cross Creek, a sub-impoundment on the Cumberland River, Tennessee. A similar estimate was obtained by Timmons and Hughbanks (2000) for Paddlefish in Kentucky Lake (1991-1992) by estimating the total instantaneous mortality for 9 to15-year-old fish (Z = 0.25) with a catch-curve. They also separated fishing (F = 0.157) and natural mortality (M = 0.093) using Baranov's catch equation (Baranov, 1918) and the exploitation rate estimate derived from tagging. Timmons and Hughbanks (2000) further stated that "*even 9% may be an overestimate, because netting and tagging by the biologists caused some mortality*".

Donabauer et al. (2009) estimated the survival rate of Paddlefish in Ozark Lake, an Arkansas River impoundment, using the Kaplan-Meyer survival model (Kaplan and Meyer, 1958) with telemetry data. With commercial and recreational harvest omitted from the analysis, they estimated two year survival rate was 0.91± 0.13, which is equivalent to an annual mortality rate of 5% and M =0.05. With the 95% confidence intervals, the upper bound for natural mortality in this study was 0.12 or a 12 % annual rate. However, the total sample size in the study was small (40 fish) and the period of observations was limited to two years.

<u>Southern stocks (LA, MS, AL)</u>

Total mortality estimates for three Louisiana Paddlefish populations that were protected by a commercial fishing moratorium instituted in 1986 ranged from $Z = 0.30$ in Lake Pontchartrain to 0.57 in the Atchafalaya River and 0.65 in Lake Henderson (Reed et al., 1992). Because exploitation of Paddlefish was minimal before and after the 1986 moratorium was established, mortality estimates for Louisiana Paddlefish were assumed to reflect natural mortality only. In light of this assumption, natural mortality of Louisiana Paddlefish was high. Reed et al.(1992) suggested that M may have been overestimated for Lake Henderson and the Atchafalaya River because of spring flooding that limited sampling in fast-flowing main channel habitats where large Paddlefish occur. In contrast, Lake Pontchartrain was easily sampled by gill nets in most areas because it is lentic and relatively shallow. Because of these differences in sampling efficiency, Reed et al. (1992) concluded that the annual mortality estimate for Lake Pontchartrain (0.30) Paddlefish was more accurate.

Rider et al. (2011) investigated Paddlefish population in the Alabama River, where the fishery was closed since 1988. Based on the catch-curve analysis for ages 6 to 17 they reported total mortality $Z = 0.345$ (29% annual rate). All age classes used in the analysis were subjected to natural mortality only, thus an estimate of total mortality was assumed to be that of natural mortality.

<u>Additional estimates of natural mortality derived in this study</u>

Generally, there is sufficient uncertainty in most natural mortality estimates and the effects of errors in M can be significant, leading to erroneous interpretation of the dynamics of the stock. Many studies (Cubillos et al., 1999; Gislason et al., 2010; Maunder and Wong, 2011) reported standard errors to be 50% to 200% of the estimate or worse. To address the issue of uncertainty in M estimates, many authors suggested using the results from multiple estimators to provide an understanding of their uncertainty (Gunderson et al., 2003; Simpfendorfer et al., 2005), and review the range of estimates in search of commonality and overlap (Hewitt et al., 2007). Thus, rather than relying on single values, the assessments may explore alternative values of M spanning the plausible range as suggested by Zhang and Megrey (2006), or may use the average of the outputs of multiple estimators (Brodziak et al., 2011).

We attempted to derive estimates of natural mortality on a stock by stock basis using as many methods of natural mortality estimation as possible, given the availability of the data. These estimates were further reviewed in terms of their appropriateness or "believability" with respect to other life

history parameters or stock exploitation history. The following methods were considered in this study to generate natural mortality estimates for initial evaluation.

Methods based on maximum observed age.

Sekharan, 1975

Sekharan (1975) assumed that, in the absence of exploitation, 1% of individuals would reach the known maximum age T_{max}. This is equivalent to:

$$\frac{N_{T \max}}{N_0} = \frac{1}{100} = e^{-T \max M}$$

Solving for M:

$$M \approx 4.6/T_{max}$$

Hoenig, 1983

Hoenig (1983) found that M was inversely correlated with longevity across a wide variety of taxa and recommended use of the following predictive equation relating the maximum age observed in the stock (t_{max}) to M:

$$\ln(M) = 1.44 - 0.982 \ln(t_{max})$$

Because both Z and t_{max} were observed with great uncertainty, Hoenig's (1983) analysis used a geometric mean regression which resulted in :

$$Z = 6.99 t_{max}^{1.22}$$

Hewitt and Hoenig (2005) showed that by solving the above equation for M one can arrive at :

$$M \approx \frac{4.22}{t_{max}}$$

The value of 4.22 in the above equation approximately corresponds to $-\ln(0.015)$, indicating that the average longevity for stocks in the data set used by Hoenig (1983) is the age at which about 1.5% of the stock remains alive.

The rule of thumb method (Hewitt and Hoenig, 2005)

The rule of thumb (Hewitt and Hoenig 2005) is a simple method that consists of determining the value of M such that leads to selected % of survival (P) of the animals in the stock to the age t_{max} . A popular assumption that 5% of animals should survive to t_{max} thus leads to:

$$M \approx \frac{3}{t_{max}}$$

Life history invariants

Various life history methods are based on a general theory that a species' life history has evolved to maximize lifetime fecundity through tradeoffs among reproduction, growth, and survival (Roff 1984).

Roff's first method (1984)

While exploring the relationship between life history parameters, Roff (1984) related natural mortality to age of maturity (t_m) and growth coefficient K as:

$$M \leq \frac{3K}{e^{Kt_m} - 1}$$

Note that this estimate was considered as an upper bound of M. When K t_m is small, it reduces to:

$$M \approx \frac{3}{t_m}$$

Roff's second method

Following his first estimator, based on t_m, Roff (1984) also derived:

$$M = \frac{3KL_\infty(1 - l_m / L_\infty)}{l_m}$$

Alverson and Carney

Alverson and Carney (1975) showed that assuming isometric growth, which is described by the VB curve with $t_0 = 0$, while natural mortality follows the exponential model, the year class reaches maximum biomass at time t_{mb}:

$$t_{mb} = \frac{1}{K}\ln(\frac{M + 3K}{M})$$

They approximated the relationship between t_{mb} and T_{max} as $t_{mb} = 0.38 \, T \, T_{max}$ using data on 63 fish populations. This can be solved for M as:

$$M = \frac{3K}{e^{K 0.38 T \max} - 1}$$

Jensen

By assuming that age at maturity is equal to the age at the inflection in the VB growth equation for growth in weight, Jensen (1996) was able to determine the constants of Roff's (1984) equation for age at maturity (t_m), which is based on maximizing lifetime fecundity through tradeoffs among reproduction, growth, and survival: $Mt_m = 1.65$ and $M/K = 1.50$ which can be used to estimate M:

$$M = 1.65/tm$$

and

$$M = 1.5K$$

Charnov and Berrigan

Charnov and Berrigan (1990) estimated that average female adult lifespan, t_a, averages 45% of t_m in fish and shrimp, while suggesting that $t_a = 1/M$. Hewitt et al. (2007) noted that following Charnov and Berrigan's findings one can arrive at:

$$M = \frac{2.2}{t_m}$$

Rikhter and Efanov

Rikhter and Efanov (1976) suggested that age of maximum biomass could be approximated as the age at 50% maturity. Based on a regression using prior data on only 14 fish populations, they derived:

$$M = \frac{1.521}{t_m^{0.72}} - 1.55$$

The coefficients are dependent on the number of species used in the regression approach. Because the relationship was based on 14 species, the appropriateness of the relationship for species not used in the analysis is untested.

Cubillos' Estimator

Cubillos et al. (1999) applied Hoenig's method but they substituted a calculated age at 95% L_∞ for observed T_{max}:

$$T_{95\%} = t_0 - \frac{\ln(0.05)}{K}.$$

and

$$M = [t_0 - \frac{\ln(0.05)}{K}]^{-1.01}$$

Empirical regressions

Pauly

One of the earliest empirical analyses was conducted by Pauly (1980), who regressed natural mortality on the VB growth rate (K), asymptotic size (either weight or length), and water temperature (T) to develop a formula for estimating M based on data from 175 populations (almost all teleosts):

$$logM = -0.0066 - 0.279 \log L_\infty + 0.6543 \log K + 0.4634 \log\tau$$

where τ is the average annual temperature C, L_∞ and K are VB growth parameters. This regression shows the negative relationship between asymptotic size and positive relationship with growth rate and temperature, which is consistent with theory and experimental data. This is one of the most frequently used estimators when direct estimates of natural mortality are not available.

Jensen – Pauly.

Jensen (2001) re-examined Pauly's Estimator in the light of advances in life-history theory. He repeated the regression analysis and revised the model to:

$$\log M = 0.66 \log K + 0.45 \log\tau$$

or

$$M = K^{0.66} \tau^{0.45}$$

Frisk's Estimator

Frisk et al. (2001) made a unique examination of relationships among the elasmobranchs, concluding that the link between M and K was significantly different from what is seen in teleosts. Through regression of data from 30 species in nine families, they arrived at an expression was:

$$lnM = 0.42lnK - 0.83$$

or

$$M = 0.436K^{0.42}$$

though they also found that M/K in the Rajidae was statistically indistinguishable from the relationship in teleosts and indicated that some other families similarly resembled teleosts in this respect. Recognizing that this regression was developed for elasmobranchs specifically, we wanted to evaluate its potential applicability to Paddlefish.

Gunderson

Gunderson and Dygert (1988) developed a linear relationship between natural mortality and the gonadosomatic index (GSI=ovary weight/ somatic body weight) and Gunderson (1997) updated the relationship using 28 stocks of fish to give:

$$M = 1.79GSI.$$

Ralston's Estimator

Ralston (1987) developed a growth (K) based estimator for M specifically for snappers and groupers. Using prior data from 19 populations in an arithmetic mean regression, he found:

$$M = 0.0189 + 2.06K$$

or

$$M \approx 2K$$

Ralston (1987), however, preferred a geometric mean regression, rendering the estimator as:

$$M = 0.0666 + 2.52K$$

or

$$M \approx 2.5K$$

Pauly and Binohlan (1996) offered an updated version, which they termed the 'Ralston Method II', based on data from 29 populations of snappers and groupers:

$$M = 0.1778 + 3.1687K$$

Recognizing that these regressions were specific to the lutjanids, we included both methods for consideration based on similarity in growth pattern – fast growth in early ages, achieving near asymptotic sizes by age of maturity, slow growth for adults, high longevity.

There are a number of other methods available in the literature that were not considered in this analysis due to the fact that they were insignificant variations of methods listed here (Djabali et al., 1993; Pauly and Binohlan, 1996; Zhang and Megrey, 2006), relate mortality to specific size of fish (Peterson and Wroblewski, 1984; Lorenzen, 2000) or are based on predation estimates (Gislason et al., 2010).

Results

A series of input parameters required by each method considered were obtained for Paddlefish stocks with available data. The inputs included maximum observed or imputed age, von Bertalanffy growth parameters K and L_∞, age and size at maturity, mean annual ambient temperature, and gonadosomatic index (Table 2.9.1). The summary of the estimates by the stock and method of estimation is presented in Table 2.9.2. The range of natural mortality estimates was rather large, from 0.01 to 1.73, with extreme values on both ends being unrealistic (Table 2.9.2, Figure 2.9.1).

Upon initial evaluation it appears that both of Ralston's empirical regressions produced a large portion of estimates that are clearly too high and therefore were eliminated. We also eliminated Gunderson-based estimates as those solely relied on a value of GSI index. As shown by Scarnecchia et al. (2008) and Scarnecchia et al. (2011), GSI for female Paddlefish increase through age from near zero values to a maximum of 0.25 or 25% at the peak of reproductive ability. According to the Gunderson estimator, the natural mortality would be increasing proportionally to GSI with age from 0.18 to 0.45 as the GSI increases from 0.1 to 0.25. An increase in natural mortality for fish in prime reproduction age does not seem to be a biologically reasonable scenario. Based on this consideration, estimates by Gunderson's method were also eliminated. Further evaluation of remaining estimates was completed on a regional basis.

Northern stocks.**(ND, SD, NE)**

We developed estimates of natural mortality for the Yellowstone River, two impoundments of the Missouri River: Lake Sakakawea and Lake Francis, and an unimpounded, unchannelized stretch of the Missouri River below Gavin's Point Dam, South Dakota-Nebraska. The estimates can be roughly split into two groups in terms of range of values: $M <= 0.1$ and $0.1 < M < 0.3$ (Figure 2.9.2).

All methods that are based on maximum age (Sekharan, 1975; Hoenig, 1983; Hewitt and Hoenig, 2005) as well as the method of Alverson and Carney (1975) produced low estimates of M (<0.1). Most of the Roff and Richter − Efanov estimators resulted in low M as well, with the exception of the Missouri River (Rosen, 1982 data). The remaining group of methods produced estimates mostly in the range of 0.15-0.28. In evaluating the plausibility of various estimates, we note that the maximum age-based methods are the least ambiguous (at least with respect to the upper limit of M), as long as age determination is reliable. Although complete validation of current ageing technique using dentaries (jawbones) has not been done, there is a significant evidence that fish in this populations live up to age 55 and possibly longer (Scarnecchia et al., 2006; Scarnecchia et al., 2011). Significant longevity logically requires a low mortality rate, and considering the evidence of the consistent presence of fish over age of 40 and 50 (at least in the Yellowstone River and Sakakawea Lake), estimates of M produced by maximum age-based methods are most likely. The estimates based on the other methods rely primarily on empirical relationships derived from a wide range of species, and Paddlefish might be deviate from the general relationship. It is worth noting, however, that the method of Pauly (1980) was reported as one of the most reliable ones in two independent reviews of methods of natural mortality estimation (Kenchington, 2013; Then, 2013). Pauly's method resulted on M values 0.16-0.27 for northern stocks which clearly is well above the M expected based on observed longevity. The only empirical estimate that supports the high estimate of M produced by Pauly's method is the one reported in Runstrom et al. (2001), who estimated 0.27 for the total mortality of a protected, unexploited population of Paddlefish in the Wisconsin River using catch-curve analysis, which is similar to Pauly' estimate. However, as mentioned before, we question the reliability of the estimate due to the very short range of ages and small sample size in the study. Overall, the low range of M (0.05-0.1) appears to be best supported by the data.

Stocks in the center of distribution (MO, KY, AR, OK, TN)

Methods based on maximum age resulted in estimates of M in the range of 0.1-0.2, depending on the maximum observed or imputed maximum age. The maximum age reported for the stock from the center of species distribution range from 12 years in Lake Barkley (Bronte and Johnson, 1984) to 27 years in Grand Lake, Oklahoma (Scarnecchia et al., 2011). Correspondingly, the maximum age-based estimates of M ranged from the low of 0.1-0.14 for Grand Lake to the high of 0.15-0.23 for Lake Barkley, with other stocks estimates falling in between (Table 2.9.2, Figure 2.9.3). A similar range of M was produced by both of Roff's estimators, Alverson and Carney, and Richter and Efanov (Figure 2.9.3, Table 2.9.2.). As in the case of northern populations, the methods of Charnov and Berrigan, both of Jensen's methods, Frisk's and Pauly's regressions produced higher estimates, approximately in the range of 0.15-0.35. Pauly's method gave a wide range of 0.18-0.58, with an average of 0.27.

There are three empirical estimates of natural mortality available for the region. In the unfished South Cross Creek on the Cumberland River, Tennessee, natural mortality of Paddlefish was estimated to be less than 9% (Boone and Timmons, 1995), while Donabauer et al. (2009) estimated an annual survival rate of 5% and M =0.05 for Paddlefish in Ozark Lake, Arkansas River. In general, direct estimates of population parameters such as natural mortality are always preferable to regressions based on life history invariants. Existing estimates for the central stocks are more in line with the longevity-based estimates similarly to the northern populations. Considering that most of the stocks in the region were subjected to significant exploitation, we would expect much higher longevities than are currently reported if the stocks were left unfished at least for one generation time. Therefore, it appears that lower estimates of M are more likely. However, because there is still some uncertainty in true estimates of M, we will be considering the upper range of M as well in order to evaluate potential effect on reference points and consequences to management decisions.

Southern stocks (LA,TX, AL).

The maximum reported age of Paddlefish in Louisiana (9 to 14 years – Reed et al., 1992) and Alabama (9 to 17 - Hoxmeier and DeVries, 1997; Lein and DeVries, 1998; Rider et al., 2011) is generally lower than in the central region and much lower than that in the northern region. Consequently, maximum age-based methods estimates were generally higher than those for the northern and central regions and varied in the 0.15-0.3 range. As with northern and central region stocks, both Roff estimates, Alverson and Carney and Rikhter and Efanov methods performed

similarly to the maximum age based methods. However, Roff's estimators for the Louisiana stocks produced M values at or below 0.1. As in other stocks, the remaining group of methods produced higher values of M, ranging from 0.2 to 0.45. The Pauly method estimates varied substantially by stock from 0.14 to 0.58 and an average of 0.28. Two empirical estimates based on age structure (catch-curve analysis), one for a lightly exploited stock in Lake Pontchartrain (M=0.3) and one for an unexploited population in the Alabama River (M=0.35), appear to be closer to the upper range of our estimates and above the maximum age-based estimates (Table 2.9.2, Figure 2.9.4). Overall, the natural mortality of southern stocks of Paddlefish appears to be higher than in the central and northern regions, with a lower bound of M around 0.15 and upper bound close to 0.35.

Summary

As with many other data-poor stocks, the available options to estimate natural mortality are generally constrained by the empirical estimators constructed from surrogate information on life history parameters. In a recent, extensive comparison of methods for natural mortality estimation, Then (2013) concluded that the updated Hoenig (1983) model had the highest predictive ability, followed by the updated Pauly, Jensen and Alverson-Carney methods. Temperature did not appear to be an important predictor in the updated Pauly model. In the analysis where various methods were tested on species with "known M", Kenchington (2013) made similar conclusions, noting that the T_{max}–based estimators performed well, while those estimators that rely on ecological or life history theory to generate single M values, including all those that build on ages other than T_{max}, generally performed poorly. These conclusions further support using longevity-based methods in selecting natural mortality estimates for Paddlefish. It is worth noting that longevity-based estimators estimate the total mortality rate (Z). If other sources of mortality are present, such as fishing, longevity-based estimators are expected to have a positive bias for estimating M.

It the face of large uncertainty, it is generally recommended not to rely on a single estimator, but to review the strengths and weaknesses of various methods. The potential management consequences of the high uncertainty in estimated M should be thoroughly explored in the assessment. Kenchington (2013) recommends that none of the estimators based on life history invariants should be used unless its input parameters can be estimated with reasonable confidence, in particular an estimate of K. He further warns that these estimators should not be used for fish with long adult lives following rapid early growth, which appears to be the case for Paddlefish.

The greatest weight of evidence (reported tests of the methods on one hand and reliability of age determination for Paddlefish on the other hand) supports the estimates for the group of methods based on the maximum observed age. Generalizing by the region, one can assume an average longevity of 50-60 years for the northern region ($0.05 < M < 0.10$), at least 25-30 years for the central region ($M = 0.10$-0.18) and at least 15-20 years ($M = 0.15$-0.31) for the southern region. Available direct estimates of mortality for the central region ($M = 0.05$-0.09), however, support the lower end of the estimates, which is closer to the ones in the north. Nevertheless, considering that a group of methods, including the method of Pauly, was shown to perform as a reasonably good predictor, and the empirical estimate of M for at least one unexploited southern stock (Rider et al., 2011) was more similar to the Pauly's method, we retained the high-end range estimates as potential alternatives. We then evaluated the effect of higher M estimates through a sensitivity analysis by completing further analyses such as Yield Per Recruit (YPR) and Spawner Per Recruit (SPR) with various levels of M, followed by a discussion of the possible management consequences of using these various M.

2.10. Total Mortality Rate Estimation

Yearclass curves

We estimated the total instantaneous mortality rate and selectivity from tag return data of stocked fish from the reach Lake Francis Case reach using yearclass curves (Cotter et al. 2004). Yearclass curves are a form of catch curve analysis that allows estimation of selectivity (i.e., relative vulnerability at age) because multiple cohorts are analyzed simultaneously. This reach was the only one for which enough data were available to conduct the analysis. The data were the catch at age of stocked fish with coded wire tags. Age was calculated from the difference between the year of capture and the year of the release. Adequate numbers of observations were available for the period 1995-2011 for the 1990-1995 yearclasses.

We used an exponential mortality model for the relative abundance of each cohort at age,

$$N_{a+1,t+1} = N_{a+1,t+1}e^{-Z},$$

where N was relative abundance, and Z was the total instantaneous mortality rate. The initial relative abundances of each age class were estimated parameters, and a single Z was estimated across all ages and years. The observation model included age-specific selectivity (s_a) and year-specific catchability (q_t, or relative levels of effort),

$$\hat{C}_{a,t} = s_a q_t N_{a,t},$$

where $\hat{C}$ was the estimated catch at age in a given year. Selectivity at age and catchability for each year were nuisance parameters that were estimated. Ages 11 and older were assumed to have a selectivity of one because age-specific selectivity estimates of these ages were unstable.

Parameters were estimated using a maximum likelihood approach (Hilborn and Mangel 1997) by minimizing the reduced negative log likelihood function (-L) assuming lognormal errors in the catch at age,

$$-L = \frac{n}{2} log \left(\sum_t \sum_a \left(log \left(C_{a,t} + 0.1 \right) - log \left(\hat{C}_{a,t} + 0.1 \right) \right)^2 \right)$$,

where n was the number of observations. Small constants were added to the observed and predicted catches to avoid taking the logarithm of zero. The estimated parameters of the model were the average Z during 1995-2011, relative abundance at age in 1995 (except for the 1990 cohort which was fixed to 100), selectivity at age for ages 3-10, and catchability for each year.

The estimated total instantaneous mortality rate was 0.177 per year (95% CI 0.143-0.219 per year; Table 2.10.1). The model had some difficulty because there was substantial interannual variability in the catchability (or effective effort; Table 2.10.1). The model estimated that Paddlefish were fully selected by about age 5 (Figure 2.10.1).

Year-specific catch curves

We conducted year specific catch curves (Ricker 1975) for all the systems for which we had age data from a survey or the harvest including waters of Arkansas from data provided by Jeff Quinn for 2003 and 2004 (years pooled) and data from Jim Garvey's study in the Mississippi River (from Arkansas and Missouri). We conducted catch curve analyses using the ages from one older than the age with the peak catch to the oldest age in each data set. Because there were several observations of age classes with zero catches in the Garvey data, 0.5 (1/2 the lowest observed value) was added to each observed catch before taking the natural logarithm.

Estimated total instantaneous mortality rates varied among systems (Table 2.10.2). The Z estimates varied from a high 1.35 per year in Arkansas during 2003-2004 to 0.5 per year in both areas from the Garvey study. All of the estimates were quite imprecise, which can be seen in the wide confidence intervals about the estimates. This is due to the generally small number of ages included in each system.

Length-based analyses

Some systems did not have either enough or appropriate data to use age-based methods to estimate mortality, but they did have estimated length composition of the commercial harvest. In these cases we applied a length-based catch curve analysis which modeled the expected size distribution of the catch under assumptions about the distribution of length at age and a minimum size limit. The approach begins with an age-structured model for relative abundance,

$$N_{a+1} = N_a e^{-Z},$$

where N_a is relative abundance at age a, and Z is the total instantaneous mortality rate. Relative abundance by 1 in length bin was then estimated using the parameter values from the age-based VB growth model. The estimated proportion of age a individuals in length bin l ($\hat{p}_{a,l}$) was

$$\hat{p}_{a,l} = \Phi(l+1) - \Phi(l),$$

where Φ was the cumulative distribution function for the normal distribution. The mean length at each age was estimated from either the appropriate reach or basin level parameters from the age-based VB growth model. The standard deviation in length at age was 2.49 in from the age-based VB growth model. The estimated catch (C) for a 1-in size bin was the sum over ages of the product of the proportion of age-a in size bin l, the relative abundance of age a, and the selectivity of size l (s, 0 below the minimum size limit and 1 above),

$$C_l = \sum_a \hat{p}_{a,l} N_a s_l.$$

The model then compared the estimated and observed proportion of the catch in each size bin above the minimum size limit using a multinomial distribution,

$$-LL = \sum_y n_y \sum_l p_l \log(\hat{p}_l),$$

where -LL was the negative log likelihood, n_y was the sample size in year y, p_l was the observed proportion of the catch in length bin l, and $\hat{p}_l$ was the estimated proportion of the catch in length bin l. Only a single Z was estimated across all the years for which data were available for a system because

the model assumes an equilibrium age and size distribution of the population and catch. The model used a maximum size bin of 45 in for all fish 45 in and larger.

The estimates of the total mortality rate differed substantially among systems (Table 2.10.3). The highest estimated mortality rate was in the Sunflower River, 1.02 per year, and the lowest was in Kentucky Lake, 0.3 per year. Most of the estimates were in the range of 0.5-0.7 per year, which is likely higher than twice the natural mortality rate.

Discussion

The length-based approach to estimating mortality rates has a number of important assumptions to consider. First, the model relies on equilibrium assumptions about the age and size structure, similar to age-based catch curve analyses. It is likely that mortality rates and recruitment are not constant, which will influence this method in unknown ways. The model also assumes that the number of fish measured represents a random sample of fish from the catch. While the methods for sampling the catch were not provided, it is likely that the samples from the catch were not completely random (e.g., all vessel's catches at a landing were sampled on a given day). Non-random sampling will tend to cause the SEs of the estimates to be too precise, but could also bias the estimates depending on the nature of the sampling approach.

2.11. Selectivity Estimation

We applied the SELECT approach described in Millar and Fryer (1999) to estimate the size selectivity of gillnets for Paddlefish using data from a rotenone study in Arkansas conducted during 2010. We modeled selectivity as an increasing logistic function of length,

$$s_l = \frac{1}{1 + e^{-\alpha(l - l_0)}}$$

where l was the midpoint of each length bin, and α and l_0 were the parameters of the logistic curve. We estimated the parameters using a maximum likelihood approach by minimizing the negative log likelihood function (-L, Hilborn and Mangel 1997),

$$-L = \sum_l k_l \log(s_l) + (n_l - k_l)(1 - s_l),$$

where k_l was the number of Paddlefish caught in the gillnet in a length bin and n_l was the total number caught in the gillnet and with rotenone. Constants in the negative log likelihood function were removed to simplify the estimation.

Gillnet selectivity increased with increasing length (Figure 2.11.1). A selectivity of 0.5 was reached at about 800 mm, and selectivity increased fairly rapidly between 600 and 1000 mm).

2.12. Additional methods to estimate fishing mortality and population size

Many stock assessment approaches exist that could be applied to Paddlefish. After examination of the available data, relatively few approaches will be able to be broadly applied to Paddlefish. Initially we had proposed to apply a couple of methods that only required a catch time series, such as stock reduction analysis (SRA) or depletion corrected average catch (DCAC). SRA requires a time series of catch for the full history of the fishery. This is not available for Paddlefish in any system to our knowledge. Additionally, SRA and related methods such as depletion-based stock reduction analysis (DB-SRA) assume that productivity of the stock has been constant over time. This assumption is likely violated because of changes to the system caused by damming and other alterations in the watershed. Statistical techniques that use the age structure of the catch together with total catch and at least one index of abundance are commonly used to estimate stock size, historical fishing mortality rates, and to set catch limits or other fishery regulations. However, there are few systems that have the available data to apply these approaches (catch-at-age for at least a decade and associated indices of abundance), and we were not provided the data for the systems for which the approach could potentially be applied. Because of the length of time series necessary to apply these methods (at least a decade of an index of abundance and age-structured catch data), it is not likely that these approaches could be applied broadly in the near future. In fact, very few jurisdictions routinely sample the fishery catch for its age composition or even its size composition. However, if size composition data are available for the fishery catch, either length-structured models or age- and length-structured models could be applied. Several jurisdictions appear to be collecting the necessary size composition data from the harvest to apply these models. With continued effort for several more years, enough data could be available to attempt this type of approach (much like statistical catch - at - age models they require at least a decade of data). However, at least one index of abundance is also required for this approach. That index of abundance could come in the form of a fishery independent

survey that is conducted annually (this option would provide the most and probably best information), or from a fishery dependent time series, such as catch per unit effort. Using fishery dependent indices of abundance usually requires high quality estimates of effort and modeling approaches that consider that fishing effort is not random (i.e., fishery dependent CPUE is likely not proportional to stock size).

3. Biological Reference Point Estimation

3.1. Yield per Recruit and Spawning Potential Ratio

Optimum yield from a population in equilibrium conditions can be estimated using a yield per recruit (YPR) modeling approach. YPR models are used to calculate the theoretical value of yield in weight that can be achieved at selected fishing mortality from a year class of fish during its lifetime. By repeating such calculation for a series of fishing mortality rates one can find the maximum yield that can be obtained from the population and a corresponding fishing mortality rate, F_{max}. By selecting F_{max} as a target fishing mortality for a particular fishery, one can try to maximize the long-term yield from a population. For this reason, the F_{max} concept was very popular in the past as a reference point used in fishery management initially as a target and later, when a precautionary approach was developed, as a limit. F_{max} has been replaced as a target by other reference points because it does not explicitly include information on maturation or reproduction, which is necessary for sustainability. Another reference point associated with YPR models is $F_{0.1}$ (fishing mortality at the point on the YPR curve with slope equal to 0.1 of the slope at the point of origin). $F_{0.1}$ is often used rather than F_{max} because it is more conservative and presents a lower risk of fishing at unsustainable levels (Doubleday et al. 1984; Andrew and Butterworth 1987; Hilborn and Walters 1992). While it is recognized that the requirement of equilibrium (keeping all model parameters constant) is not likely to be satisfied, it generally believed that the model results can be valid and useful for management in the long-term aspect as long as the effort is made to maintain a constant F. When direct estimates of population productivity (MSY, F_{msy}, steepness of stock recruitment relationship) are not available, the YPR models and associated spawning potential ratio (SPR) calculation remains a frequently used tool to guide sustainable management.

Another analysis normally completed in parallel with the YPR is the calculation of the spawning stock biomass per recruit (SSBR) and SPR. Spawning stock biomass per recruit is an estimate of total contribution to the spawning stock by each recruit throughout their lifetime. SSBR analyses use constant schedules of mortality, maturity, and spawning weight at age for a cohort. Under conditions of no fishing mortality, 100% of a stock's spawning potential is obtained. As fishing mortality increases, SSBR decreases, as more spawning opportunities are lost over the lifetime of the

cohort. The reduction in SSBR relative to the unfished level can be reflected as a percentage of the maximum spawning potential (*MSP*) SPR.

For example, a fishing mortality rate denoted $F_{35\%MSP}$ would allow a stock to attain only 35% of the maximum spawning potential which would have been obtained under conditions of no fishing mortality. This model gives rise to reference points of the form of e.g., $F_{20\%SPR}$ or $F_{35\%SPR}$, representing fishing mortality that will reduce SPR to 20 or 35% of the unfished population. Values in the range $F_{20\%}$ to $F_{30\%}$ have frequently been used throughout the world to characterize recruitment overfishing thresholds while values in the range $F_{30\%}$ to $F_{40\%}$ have been used as proxies for F_{MSY} (Rosenberg et al., 1994). Therefore, we chose to report $F_{30\%}$ and $F_{40\%}$ as candidate reference points. However F values in the full range of %SPR are available as an output of the model.

Methods

YPR and SPR calculations for all Paddlefish stocks under consideration were completed using a custom written code in R (R-project, 2013) as well as the YPR module in National Oceanic and Atmospheric Administration Fisheries Toolbox version 2.7 (NOAA 2008). We used a modified version of the Thompson-Bell YPR model (Thompson and Bell 1934; Ricker 1975).

$$\frac{Y}{R} = \sum_{a=1}^{t\max} N_a w_a \frac{F*S_a}{F*S_a + M}(1 - e^{-(F*S_a+M)})$$

where Y/R is yield per one recruit in weight (kg); *a* – age of fish; t_{max}- maximum age; N_a - abundance at age, w_a- mean weight at age *a*; *F* is fishing mortality at age *a*; S_a – selectivity at age, and *M* – instantaneous natural mortality. To determine F_{max} we applied a range of fishing mortality values from 0 to 1.0 with a step of 0.01. We also calculated $F_{0.1}$. In addition to the standard YPR calculation, we calculated an eggs per recruit number that would allow estimating maximum yield in terms of roe, rather than flesh.

We estimated SSBR and SPR following Gabriel et al. (1989). The spawning stock biomass at each age is calculated as the number alive multiplied by the fraction mature multiplied by the weight of an individual:

$SSB_a = N_a PM_a e^{-Z_a}$ where SSB_a is the spawning stock biomass at age; N_a is the number of fish alive at the start of the year at age a; PM_a is a proportion of fish mature at age a; Z_a is the total mortality of age a fish between the start of the year and the spawning time

$$Z_a = (S_a F + M)\Delta T$$

where S_a is the selectivity for age a (fraction of full F applied to age a), M is the natural mortality, and ΔT is the time between the start f the year and spawning (as a fraction of a year). The total contribution of a cohort to the spawning stock biomass over the cohort's lifetime is the sum of the cohort's contributions at each age:

$$SSB_{total} = \sum_{a=1}^{t\,max} SSB_a$$

and spawning stock biomass per recruit is

$$SSBR = \frac{SSB_{total}}{N_1}$$

where N_1 is the number of recruits (age 1 fish).

A maximum spawning stock biomass per recruit is obtained under conditions when the fishing mortality is zero (F = 0). An increase in fishing mortality results in reduced levels of SSBR. A spawning potential ratio (*SPR*) is calculated as a ratio of SSBR at selected level of *F* and the *SSBR* at zero fishing mortality:

$$SPR = \frac{SSBR_F}{SSBR_{F=0}}.$$

Input parameters

YPR and SPR calculations were completed for a subset of stocks to be representative of the region (northern, central and southern), age structure, longevity and growth rates. The estimates were produced for Paddlefish stocks of Lake Sakakawea (Missouri) and Lake Francis Case (Missouri), Kentucky Lake, Arkansas River pools combined, Grand Lake (OK), Lower Mississippi and Alabama Rivers.

Age structure

The number of age classes used in the analysis of each stock generally corresponded to the reported or estimated maximum age (see Maximum age section of this report). For the Missouri River basin, the Lake Sakakawea stock was modeled with 60 and the Lake Francis Case with 50 age classes. Two options with 21 (corresponds to M= 0.2) and 30 (M=0.14) age groups were considered for Kentucky Lake, Arkansas River (pools combined), Grand Lake and Lower Mississippi River. The Alabama River representing southern stocks was modeled with 17 age classes with last age treated as a plus group.

Natural mortality

Natural mortality was selected for each stock was based on the review of natural mortality estimates derived from various methods (see section 2.9). For the northern stocks with high longevity a low level of M was found to be justified, therefore for Lake Sakakawea and Lake Francis Case an M value of 0.07 was used. For the stocks from the central area of distribution, a range of M values was used (0.07, 0.14 and 0.2) reflecting the uncertainty in life expectancy. The southern stock of Alabama River was modeled with M=0.25, while for the Lower Mississippi river an M=0.14 was used as justified by the age structure (Table 2.9.1). For each stock additional YPR model runs were made with a range of natural mortality values below and above the selected values to investigate model sensitivity to the estimate of natural mortality.

Weight at age

Weights at age for each stock were calculated with two steps. First, length at age for each stock was estimated based on corresponding Von Bertalanffy growth parameters (Table 2.5.4). Then the stock specific parameters of length weight relationship were used to estimate mean weight at age (Table 2.6.1).

Maturity

Stock specific maturity ogives estimated in this study (see Maturity chapter) were applied correspondingly (Table 2.7.9).

Selectivity on F

Selectivity parameter (sometimes termed as "partial recruitment") represents a fraction of a maximum fishing mortality experienced by different ages in the population.

Selectivity represents the effects of a combination of factors such as fish size and behavior, type of fishing gear, and environmental factors on the probability of fish being captured. Throughout the range, both commercial and recreational Paddlefish fisheries are managed primarily through the establishment of minimum size limits, although size slots, seasons and gear restrictions are also used for management. Nonetheless, minimum size is considered to be the primary control measure of fishery removals, and the legal minimum size has been increased multiple times in various regions with the goal of reducing fishing mortality and providing greater protection to spawning fish.

To model selectivity as a function of the size of the fish, we assumed a knife edge length-based selectivity, which means that fish below the minimum legal size are not subject to fishing mortality, while fish equal or larger than minimum size will experience the full fishing mortality. Because the YPR model is age structured, selectivity for each age needs to be estimated. The selectivity for each age group is calculated as the fraction of fish in the age class that are at or larger than minimum harvestable size. To estimate this fraction, we assumed that size at age for each age group is distributed normally with the mean length of L_a and a variance δ_a from the VB growth models. The proportion of fish in the age group a with the size at age distributed normally with the mean length of L_a and a variance δ_a that are larger than minimum size x is estimated as:

$$1 - F(x)$$

where F(x) is the value of the cumulative function of normal distribution at value x (which is a minimum size in our case)

$$F(x) = \Phi(\frac{x - \mu}{\sigma})$$

and

$$\Phi(x) = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^{x} e^{-t^2/2} dt$$

We estimated mean size at age, variance and proportion of fish equal or larger that minimum size for each stock under consideration for a range of minimum sizes from 32 to 38 inches (EFL).

Thus, series of selectivity (partial recruitment) vectors by age were calculated for various minimum sizes for each stock. An example of partial recruitment vectors corresponding to various minimum sizes is presented in Figure 3.1.1 and in Table 3.1.1.

Results

The output of the YPR/SPR model includes an estimate of catch in numbers, YPR, total biomass, total numbers, spawning stock numbers, SSBR, SPR, mean age, mean generation time and expected number of spawnings. The principal variables of interest were F_{max}, $F_{0.1}$, $F_{30\%}$ and $F_{40\%}$.

Northern stocks

Yield per recruit for northern stocks has a well-defined maximum at lower minimum sizes (32-34 inches) that is achieved at the modest levels of F (0.18 - 0.21 for Lake Francis, and 0.26 -0.34 for Lake Sakakawea, Tables 3.1.2, 3.1.3, Figures 3.1.2 – 3.1.3. With an increase in minimum size, yield per recruit curve becomes asymptotic, which leads to high F_{max} values, particularly for the Lake Sakakawea stock. The asymptotic shape of the YPR curve indicates that near maximum yield can be obtained at a wide range of F. However, increasing in F always leads to a decline in reproductive potential measured by SPR. Fishing mortality expected to reduce SPR to 40% is not sensitive to the minimum size, slightly increasing from 0.06 at the minimum size 32 inches to 0.07 at minimum size of 38 inches for Sakakawea stock and from 0,05 to 0.06 for Lake Francis Case. Similarly $F_{30\%}$ ranged slightly from 0.08-0.10 and 0.06 -0.08, respectively. To maintain the population at 30% SPR, an annual exploitation rate should not exceed 6 - 8 % for Lake Sakakawea and 7- 9% for Lake Francis Case, while for the 40% SPR, the exploitation rate should not exceed 4- 6% (Tables 3.1.2 and 3.1.3). A goal of maintaining spawning potential ratio at 30 or 40 % will require lower fishing mortality relative to F_{max} and will result in lower yield than YPR than at F_{max}. For example, for Paddlefish of Lake Sakakawea the YPR at $F_{30\%}$ is 75 to 84% of the yield at F_{max} (Table 3.1.2), while the YPR at $F_{40\%}$ is only expected to be 66-78% of that at F_{max}. However, such comparison is likely to overestimate percent of potentially lost yield because fishing at F_{max} will reduce the spawning stock very low levels, 2% to 0.25% SPR, and is likely to result in severe recruitment overfishing.

Stocks from the Central Region

YPR and SPR analysis was completed for a number of stocks from the central region. Results for Kentucky Lake, Grand Lake, and Arkansas River pools combined are presented in Tables 3.1.4 – 3.1.11 and Figures 3.1.4 -3.1.10. As an example, we provide a description of results for one of the stocks in the region, Kentucky Lake.

YPR and SPR analysis for Kentucky Lake was completed for a range of minimum sizes and several options for natural mortality: M=0.08 as estimated in two regional studies ($T_{max} \approx$ 50), M=0.14 ($T_{max} \approx$ 30) and M= 0.2 ($T_{max} \approx$ 21) . Under the assumption of M=0.08, which was used by Scholten and Bettoli, 2005), F_{max} was estimated to vary from 0.2 (32 inch min size) to 0.38 (38 inch minimum size). The F30% ranged from 0.10 to 0.15, about half of F_{max}, and very similar to $F_{0.1}$ values (0.11-0.13). Exploitation rates at $F_{30\%}$ are in the range of 10% (32 inch min size) to 13% (38 inch min size),   and the exploitation rate at $F_{40\%}$ is slightly lower, 7-10%.

At higher M of 0.14 ($T_{max} \approx$ 30) F_{max} rapidly increases with increase in min size and is not estimable for largest min sizes due to the monotonic rise of the YPR curve. The flat slow rising YPR curve indicates that very similar YPR can be obtained at large range of F values. However, high F values are not sustainable due to the significant reduction in SPR and subsequent expected declines in recruitment. Exploitation rates at $F_{30\%}$ are in the range of 11-17%, while $F_{40\%}$ is in the range of of 8-12%.

Increasing M to 0.2 approximately equivalent to current maximum age (21), leads to constantly rising shape of the YPR curve Figure 3.1.5 with no defined F_{max}. The $F_{30\%}$ values range from 0.16 (32 inch min size) to 0.3 (38 min size) and corresponding exploitation rate from 14 to 24%.   The more conservative $F_{40\%}$ is in the range of 0.12-0.21 with exploitation rates of 10-18%.

Overall, $F_{30\%}$ and $F_{40\%}$ are most sensitive to increased values of natural mortality. The highest YPR is achieved at lower natural mortality and it declines with increasing natural mortality. Fishing mortality that maintains 30 or 40% of SPR is higher for higher M values. All of this indicates that correct estimation of natural mortality for Paddlefish in the region is very important. If regional estimates of natural mortality in the range of 0.05 -0.09 are correct, given current minimum size limit of 38 inches the exploitation rate should not exceed 13% to maintain at least 30% of spawning potential. Under a higher M scenario that assumes that the maximum age 30 years, the exploitation rate should not exceed 17% to maintain 30% SPR.

Arkansas River Pools combined

In comparison to Kentucky Lake Paddlefish, Arkansas River Paddlefish (pools combined) appeared to be more resilient to the fishing pressure. YPR curves were asymptotic (no maximum for yield can be calculated) for nearly all M and minimum size ranges considered (Figures 3.1.7 – 3.1.9, Tables 3.1.7 - 3.1.9). At the preferred estimate of natural mortality M=0.07 (based on empirical estimate by Donabauer et al. (2009), F_{max} varied from 0.36 (32 inch min size) to 0.87 at 35 inch legal minimum size. There was no maximum for YPR at 36-38 minimum size due to monotonic increase of the YPR curve (Figure 3.1.7).

Unlike Kentucky Lake, $F_{30\%}$ was very sensitive to the minimum legal size, increasing from a low F of 0.13 at 32 inch minimum size to a high of 0.99 at 38 inch minimum size. Corresponding exploitation rates ranged from 12% to 61%. Therefore, the higher the established minimum size, the higher the fishing pressure that can be allowed to achieve the same level of SPR. Similarly, $F_{40\%}$ increases from 0.1 to 0.57 as the minimum size increases from 32 to 38 inches and exploitation rises from 9 to 42 %.

When higher M values are applied (M=0.14 and M=0.2), YPR is substantially lower than the YPR at lower M, and no F_{max} can be estimated due to a continuous, but slow, increase in YPR with F. The YPR is also more affected by the choice of the minimum size with the largest YPR obtained at the lowest minimum size (32 inches). The difference in yield could be very significant, up to 50%, particularly at higher M values, as demonstrated by the wide spread of YPR curves at various minimum sizes (Figure 3.1.8). Higher natural mortality is also often associated with greater resilience to fishing pressure with respect to the spawning potential. $F_{30\%}$ increases rapidly from 0.16 to 2.0 and beyond (Tables 3.1.8 -3.1.9). The principle cause for differences in YPR and resilience to fishing between Kentucky Lake and Arkansas River pools combined is slower growth and later maturation of Arkansas River Paddlefish that results in accumulation of spawners in larger size classes, thus allowing for higher fishing mortality to achieve a selected level of SPR.

Grand Lake

  The Grand Lake YPR analysis was completed for two levels of natural mortality, M=0.14 and M=0.20. F_{max} existed only for 32 inch minimum size at M=0.14; for all other combinations no F_{max} value could be estimated due to the monotically increasing YPR curve. The $F_{30\%}$ values were sensitive to the minimum size, however the range of $F_{30\%}$ values was much narrower (0.14 - 0.32 and 0.18 - 0.47 for M=0.14 and M=0.20). Corresponding exploitation rate values varied from 12 to 26% (M=0.14) and 15-34% (M=0.20).

  With respect to resilience to fishing pressure, Paddlefish in Grand Lake are more similar to the Kentucky Lake population than to the Arkansas River pools combined. A lower rate of fishing mortality is required to maintain the population at 30% SPR.

<u>Southern stocks</u>
Alabama River

  Results for the Alabama River are very similar to those obtained for the central region stocks with the higher M values option. The F_{max} is not estimable due to continuous slow rising YPR with the increase in F (Figure 3.1.11). Overall expected yield per recruit is low, similar to the level of YPR for central region stocks with the high M values (M=0.20). The lower minimum size produced higher YPR but requires lower fishing mortality to maintain SPR at 30% or 40% level (Figure 3.1.11; Table 3.1.13). For example, at the 32 inch minimum size, to maintain the population at 30% of maximum potential, an $F_{30\%}$ =0.27 can be applied (U=21%), while at the 38 inch minimum size $F_{30\%}$ = 1.64 and exploitation rate U=74%. Note that the F and U values here and elsewhere are for fully recruited ages (selectivity = 1) and fishing mortality and exploitation rate will be lower for age groups that are not fully recruited (selectivity < 1).

Lower Mississippi River

  Lower Mississippi River YPR analysis was done for an M=0.14 assuming T_{max}=30.
Results are similar to Alabama River, with no estimable F_{max}, and $F_{30\%}$ and $F_{40\%}$ being sensitive to the selection of minimum size. However, the range of F required to achieve 30% SPR is narrower, as the reference point does not change as much with a rise in the minimum size (Figure 3.1.12). For

example, an $F_{30\%} = 0.45$ at a 38 inch minimum size, while this value for the Alabama River stock at a 38 inch min size is 1.64. These differences are primarily driven by the differences in natural mortality values.

3.2. Egg per recruit

Traditionally YPR analysis is completed to estimate maximum yield in weight (biomass) that can be removed from a fish population on a per recruit basis and a corresponding fishing mortality that will produce this maximum. This approach evolved from the analysis of large commercial fisheries that are interested in maximizing the yield in weight. However, commercial interest in Paddlefish is primarily driven by the demand for its eggs for the caviar industry. With this in mind, it is possible to reformulate YPR model to estimate maximum yield in terms of the number of eggs that can be harvested (or roe weight) and corresponding fishing mortality that would produce this maximum yield. In our analysis this was done by substituting mean weight at age with average fecundity at age in the YPR formula:

$$\frac{Eggs}{R} = \sum_{a=1}^{t\max} N_a fec_i \frac{F * S_a}{F * S_a + M} (1 - e^{-(F*S_a+M)})$$

where fec_i is average fecundity at age.

As an example of the egg per recruit analysis, we present results for the Kentucky Lake population. As with YPR, the eggs per recruit maximum existed only for lower minimum sizes and is achieved at slightly higher values of F compared to YPR (Table 3.1.14). As minimum size increases, the EPR curve becomes asymptotic with no defined maximum (Figure 3.1.13, Table 3.1.14). However, unlike the YPR, the highest yield of eggs per recruit is obtained at the higher minimum sizes. The EPR analysis does not affect the F30% and F40% values, which are substantially lower than the values producing maximum egg yield. Thus, maintenance of 30 or 40% of spawning potential will require a fishing mortality rate somewhat lower than maximum egg yield.

3.3. Effect of gillnet selectivity

As described in the gillnet selectivity section, the probability of capturing Paddlefish by gillnet appears to be size dependent. Specifically, the probability of capture increases with increasing size of

the fish (Figure 2.11.1). Such dependence indicates unequal vulnerability of fish of various sizes to the fishing pressure, which needs to be accounted for in the YPR-SPR analyses. As an example of such correction, we used gillnet selectivity estimated in this study for the 5 and 6 inch bar mesh size based on the data provided by the Arkansas Game and Fish Commission staff. The 5 and 6 inch bar mesh size nets are typical nets that are used in the Paddlefish commercial fishery in Arkansas, Tennessee and other states, and, therefore, the estimated gill net selectivities are likely to be representative of the gillnet fishery. To avoid confusion due to the fact that the same term "selectivity" is used to describe the gill net capture probability as well as fraction of total fishing mortality in the YPR analysis, we will use the term "partial recruitment" to describe the fraction of the total mortality by age groups for the YPR analysis. To calculate the age specific partial recruitment for fishing mortality that accounts for gillnet selectivity, the sum of the products of gillnet selectivity estimates for each length group (one inch interval) and the proportion of fish of this size group within the age class was calculated:

$$P_a = \sum_{l_{min}}^{l_{max}} Sel_l P_{a,l}$$

where Sel_l is gillnet selectivity for size group l, $P_{a,i}$ is proportion of fish of size l in age group a, l_{min} is the minimum size and l_{max} is the largest size group.

To calculate age specific partial recruitment PR_a, each value of P_a was divided by the largest P_a value among all age groups:

$$PR_a = \frac{P_a}{\max(P_a), a = 1:T_{max)}} .$$

An example of the YPR and SPR modeling results with the correction for gill net selectivity for the Arkansas River is presented in Figure 3.1.14. Similar to the original analysis that accounted only for a minimum size effect and size at age distribution, the YPR curve rises monotonically. Thus no maximum for yield can be defined (within the range examined) and the YPR slowly increases with an increasing F. A comparison of $F_{30\%}$ values estimated with and without correction for gillnet selectivity is presented on Figures 3.1.15 -3.1.16. While there was little difference in $F_{30\%}$ values at lower minimum size, a lower $F_{30\%}$ value is required to protect 30% of SPR when gillnet selectivity is accounted for. Analagous calculations for the Kentucky Lake population showed very little difference after the gillnet correction was completed (Figure 3.1.16). Our results suggest that gear selectivity may

play an important role in some systems. In these cases there is a need to account for gear selectivity due to the fact that the YPR/SPR-based reference points can be rather sensitive to the gill net selectivity estimates. Ignoring the effect of selectivity may lead to inappropriately estimated biological reference points and potentially result in overexploitation. However, the interplay of growth and maturity rates may result in partial recruitment not being sensitive to gillnet selectivity, as was shown in the case of Kentucky Lake population. Because the effect of gear selectivity cannot be predicted *a priori*, an estimate of gear selectivity should be produced whenever possible and included in the partial recruitment calculation for the YPR analysis.

3.4. YPR / SPR for Recreational Fisheries

Currently sport fishing for Paddlefish is allowed in 13 states. The fish are primarily captured by snagging during the pre-spawning and spawning runs. Therefore, the recreational harvest is comprised primarily of mature male and female Paddlefish (see for example Scarnecchia et al., 2011). No published estimates are available on snagging selectivity or survivorship of fish that escaped or were released. A recent study by Brennan and Gordon (2013) reported a 100% survivorship using telemetry tags, but the sample size was very small (6 fish). Based on the information available, the partial recruitment vector (selectivity) could be based on the maturity schedule, which would assume that mature fish are selected by the fishery. For fisheries where a legal minimum size is used, the final partial recruitment calculation will be analogous to the one that we developed for the gillnet fishery with a minimum legal size. However, there are only a few states and locales with a recreational minimum size (e.g., 24 inch minimum size on Mississippi River and 34 inches on Ozark, Truman and Table Rock Lakes in Missouri).

We completed YPR/SPR analysis for two populations with significant recreational fisheries that have no minimum legal size limit: Grand Lake, OK (Figure 3.1.17) and Sakakawea Lake (Figure 3.1.18). The YPR and SPR modeling for recreational fisheries that have no size limit were modeled using the partial recruitment vector equal to the proportion of mature females at age. The focus on females is required to address the issue of reproductive potential. The analysis for Grand Lake resulted in YPR and SPR curves with no minimum size limit being very similar to the outcome when a 37 inch minimum size is imposed with corresponding $F_{30\%}= 0.15$, $F_{40\%}=0.17$, $U_{30\%}=0.13$ and $U_{40\%}=0.14$. The analysis for Lake Sakakawea indicates that the yield pre recruit will be rising with the

increase in F with no maximum and it will be somewhat lower at lower F levels, but will reach asymptotic level as F increase (Figure 3.1.18). More importantly, a notably higher F is allowed compared to any option with the minimum size that would maintain 30% or 40% MSP.

3.5. Spawning potential ratio and maximum excess recruitment

Brooks et al. (2010) proposed a method that allows direct calculation of reference points from biological data without requiring a full assessment model or fisheries data, which makes the method an attractive option for data-poor fisheries, such as the case of Paddlefish. They derived an analytical method to calculate appropriate levels of SPR, which can be used to define an $F_{\%SPR}$ as a proxy for F_{MSY}. First, they noted that harvesting theory is based on the assumption that an adult stock can produce recruits in numbers that exceed replacement. Given a stock–recruit function, it is possible to determine the point where the excess recruitment in number of individuals is at a maximum (Maximum Excess Recruitment or MER, as defined by Goodyear, 1980).

Brooks et al. (2010) showed that when the stock recruitment relationship is described using Beverton – Holt model:

$$R = \frac{bS}{1+aS}$$

where R is recruitment and S is the spawning stock numbers or biomass or total number of eggs. An estimate of number or biomass of spawner biomass per recruit that produces maximum recruitment (SPR$_{MER}$) can be obtained as:

$$SPR_{MER} = \frac{1}{\sqrt{b\phi_0}}$$

where b is the parameter of Beverton Holt stock recruitment function and φ_0 is unexploited spawners per recruit. The spawner per recruit in unfished population φ is:

$$\phi_0 = \frac{S_0}{R_0} = \sum_{age=r}^{max\,age} \mu_{age} E_{age} \prod_{r}^{ge-1} e^{-M}$$

where μ_{age} is the proportion mature at age, E_{age} the fecundity at age, r the age of recruitment, and M is natural mortality.

The denominator in the final term, which is the root of the product of unexploited spawners per recruit (φ_0) and the slope at the origin (b), is equivalent to the root of the maximum lifetime reproductive rate at low density, $\acute{\alpha}$ (Myers et al., 1997, 1999).

Therefore,

$$SPR_{MER} = \frac{1}{\sqrt{\alpha}}$$

Maximum lifetime reproductive rate, $\acute{\alpha}$, is the number of recruits produced by a recruit over its lifetime, in the absence of fishing. Therefore, if life history data are available, SPR_{MER} can be obtained analytically, without the need for an assessment model or fishery catch or effort data.

More importantly, the percent depletion of spawning stock from unfished status to the spawning stock size that produces maximum recruitment can be estimated as:

$$\frac{S_{MER}}{S_0} = \frac{\sqrt{\alpha} - 1}{\alpha - 1}$$

This provides a direct opportunity for estimating % SPR and corresponding F that will result in maximum production of recruitment. An estimate of $\acute{\alpha}$ is simply a product of unexploited spawners per recruit from standard SPR analysis (φ_0), and the slope of Beverton-Holt stock recruitment curve at the origin (the slope b is a measure of first-year survival from eggs to age 1):

$$\acute{\alpha} = b\varphi_{0.}$$

We were able to estimate φ_0 for various Paddlefish stocks, but we could not estimate *b* or survival from eggs to age 1 from life history data. The only available estimates of the survival from eggs to age 1 were the ones from the elasticity analysis that are equivalent to the survival required to keep the population in equilibrium condition ($\lambda = 1$). In equilibrium condition the maximum lifetime reproductive rate, $\acute{\alpha}$ is always equal to 1 and maximum recruitment production would occur at 50% reduction of spawning stock (MSP=0.5). However, $\acute{\alpha}$ should be higher than 1 at least for some periods of time in order for the population to be able to expand. Myers et al. (1999) investigated variability of maximum annual reproductive rate for many species and found that it is typically between 1 and 7. This number may be less for some species and more for others, but the relative constancy of the annual reproductive rate was a very important finding. Clearly, the optimal level of depletion depends on life history traits, the combined effect of which is reflected in the maximum lifetime reproductive

rate, ά. The more productive a stock, the higher the rate at which it can be exploited. A range of ά from 1 to 7 corresponds to the range of spawning stock reduction from 0.5 to 0.27 or 50 to 27% SPR. It seems reasonable to consider this range for the Paddlefish management until Paddlefish-specific parameters become available.

Although this method allows the estimation of the SPR reduction that maximizes harvest in numbers, it is only an approximation to SPR_{MSY}, where MSY reflects maximizing yield in biomass. Brooks et al. (2010) conducted a simulation study to compare the SPR_{MER} and SPR_{MSY} and corresponding fishing mortalities F_{MER} and F_{MSY}. They concluded that when all ages were fully selected, F_{MSY} was always lower than F_{MER}. This is explained by the fact that weight increases with age, so maximizing yield in weight would require allowing more fish to survive to older ages. However, if selectivity is shifted to the right of maturity curve (only larger mature fish are being exploited), the F_{MSY} may exceed F_{MER}. Similarly, they found that F_{MSY} exceeded M only when the selectivity ogive was shifted to the right of the maturity ogive. The practical outcome of these observations is that F_{MSY} is likely to be lower than F_{MER}, particularly in the case of mid to low steepness of the stock – recruitment curve. Therefore, the estimates of SPR_{MER} and corresponding F_{MER} should be viewed as upper bounds, and lower, more precautionary F reference points should be considered until stock-recruitment data are accumulated.

3.6. Elasticity Analysis

Elasticity analysis is a popular form of sensitivity analyses for matrix population models, which is widely used in conservation assessment. Elasticity analysis allows estimation and comparison of the percentage changes in population growth (λ) resulting from percentage changes in the vital rates (survival, fecundity growth) of particular classes of individuals (Heppell et al., 2000). Sensitivity analyses of life history and demographic parameters have proven useful in evaluating conservation strategies for long-lived species including sturgeons (e.g., Dixon et al. 1997; Caswell, 2000; de Kroon et al., 2000, Gross et al., 2002, Heppell, 2007; Doukakis et al., 2010), but have not previously been applied to Paddlefish.

Elasticity analyses involve matrix projection models that divide populations into classes of individuals that share similar demographic parameters (such as age-classes). Elasticity is the proportional change in population growth (λ) corresponding to a proportional change in one entry in the Leslie matrix (**A**) describing the population's fecundity and survival at age (de Kroon et al., 2000):

$$\frac{\mathrm{A}_{i,j}}{\lambda}\frac{\partial \lambda}{\partial \mathrm{A}_{i,j}}=\frac{\mathrm{A}_{i,j}}{\lambda}\frac{v_i u_j}{\langle u,v \rangle}$$

where (**A**) is the Leslie matrix, λ is population growth corresponding to a proportional change in one entry, v is the age-specific reproductive value, calculated as the first left eigenvector of the Leslie matrix (scaled to sum to 1.0), and u is the stable age distribution, calculated as the first right eigenvector of the Leslie matrix scaled to sum to 1.0. The inner product of the two vectors is denoted by (**u,v**). Elasticities are additive and sum to 1.0.

Perturbing matrix projection models and calculating the effect on λ through elasticity analyses reveals how prospective changes in the demographic parameters of any life history class will influence overall population growth rate (Gross et al., 2002). Elasticity analyses can predict how λ will change with small changes to the survival or fecundity of each age-class, allowing managers to evaluate the influence of any particular change on population growth rate. Alternatively, the models can predict how λ will change with small changes to the survival or fecundity of broader life history stages, such as juveniles or adults, allowing managers to address groups of individuals that may require similar conservation initiatives (Gross et al., 2002).

We performed the elasticity analysis for three stocks with a range of age structure and natural mortality to evaluate their response to changes in survival and fecundity - Sakakawea Lake (60 age classes), Kentucky Lake (30 and 20 age classes) and Alabama River (20 age classes). Corresponding stock specific values of weight, maturity and fecundity at age described in other chapters were used as inputs. Because no information was available to estimate survival of eggs to age 1, we used a value that resulted in $\lambda = 1.0$ given the other parameters. This value of λ implies that the population is in equilibrium with no fishing (Gross et al., 2002). We assumed survival of fish age 1 and greater was constant across ages and used the natural mortality rate calculated by using Hewitt and Hoenig (2005) method ($M = 0.07$ for Sakakawea stock, M=0.14 for Kentucky Lake and M= 0.3 for Alabama River). The Leslie matrix was assumed to apply to only females, thus, the egg production per spawning female at a given age was multiplied by 0.5 to account for eggs production by females only. Females are assumed to have a spawning interval, however, we did not model it due to the fact that spawning intervals are poorly known and vary among systems (see Maturity chapter). Fortunately, if the spawning interval is more or less constant, it has no effect on the elasticity outcomes. The model

assumes no density dependence in population dynamics and the populations are evaluated at equilibrium and at a stable age distribution.

Results

The elasticity of survival at age was highest for immature age classes for all stocks and declined with age (Figures 3.6.1. - 3.6.5) because fewer fish survive to the older ages to contribute to the population's reproductive rate. The cumulative elasticity of survival of immature (i.e., age 1 until the age of maturity) age classes was higher than that of all the adult age classes for all stocks (Figures 3.6.6. - 3.6.9), but in particular for Sakakawea Lake (Figure 3.6.8). The elasticity of fecundity multiplied by egg-to-age-1 survival was low compared with the elasticity of immature and adult survival (Figures. 3.6.6 -3.6.9). The cumulative elasticity across all age classes of fecundity multiplied by egg-to-age-1 survival was around 8 - 10%, equivalent to the elasticity of a single immature age class (Figures 3.6.5 and 3.6.9). Elasticity analysis indicated that population growth is most sensitive to the change in the survival of juveniles (cumulative elasticity 0.50 - 0.62). Population growth was affected to a smaller extent by the survival of adults (cumulative elasticity 0.33 - 0.43). Changes to fecundity have the smallest impact (Figure 3.6.9). The elasticity results suggest that when some conservation efforts are required, increasing survival of immature fish will provide the strongest response in population growth.

3.7. Selection of Biological Reference Points for Management

The long-term objectives for commercial fisheries management generally include maximizing the harvest (traditionally for the biomass), while sustainably maintaining the population. In order to achieve these long-term objectives, values of the fishing level which allows for the largest catches in weight or numbers must be estimated, while also ensuring conservation of the stocks. At the same time, excessively high fishing mortality and a low spawning stock biomass will likely negatively affect the reproductive ability of the stocks and should be avoided. The fishing mortality and biomass values used to establish target and limit levels for management are referred to as biological reference points (BRP). Biological reference points are stock-specific benchmarks that are essential

for applying the precautionary approach to fishery management. Typically, stock biomass and fishing mortality rates (e.g. B_{MSY}, F_{MSY}, and $F_{0.1}$) are computed for each stock as selected BRPs. In order to determine the stock's relative health, these BRP's are compared to current levels of stock abundance and fishing mortality. BRPs provide a means of quantitatively measuring the effect of fishing on the stock and for determining the desired level of stock maintenance. The FAO Code of Conduct for Responsible Fisheries (FAO, 1995b) identifies two categories of BRPs, target reference points and limit reference points, each having specific roles in determining stock status.

Target reference points

Target reference points are benchmarks intended to achieve specific management objectives, usually an optimum yield in weight. Examples of target reference points include F_{MSY} (fishing mortality rate associated with maximum sustainable yield), B_{MSY} (stock biomass associated with maximum sustainable yield), and SSB_{MSY} (spawning stock biomass associated with maximum sustainable yield). When these reference points cannot be estimated, their proxies are used, such as $F_{0.1}$ (proxy reference point which yields near maximum yield per recruit (YPR) with significantly less effort than needed to achieve maximum YPR), fishing mortality corresponding to a selected percent of maximum spawning potential (SPR; e.g. $F_{30\%}$ - fishing mortality rate producing 30% of the maximum spawning potential in the absence of fishing, $B_{30\%}$ - associated stock biomass, and $SSB_{30\%}$ - associated spawning stock biomass).

Limit reference points

Limit reference points are benchmarks intended to constrain harvests so that the stock remains within safe biological limits. Ideally, the probability of exceeding limit reference points should be low. When a limit reference point is exceeded, it triggers significant restrictions on the fishery in order to rebuild the stock. Examples of limit reference points include F_{MSY}, $F_{20\%}$ (fishing mortality rate producing 20% of the maximum spawning potential in the absence of fishing), $SSB_{20\%}$ (associated spawning stock biomass), F_{MAX} (fishing mortality rate that yields maximum yield per recruit), SSB_{MAX} (associated spawning stock biomass), F_{SSBmin} (fishing mortality rate that prevents

the SSB from declining below the minimum observed SSB), and SSB_{min} (associated spawning stock biomass).

Control rule concept.

      Biological reference points most frequently are used in fishery management to establish control rules. A control rule describes a variable over which management has some direct control as a function of some other variable related to the stock (Restrepo et al., 1998). For example, it can describe how fishing mortality (F) should change depending on the spawning biomass of the resource. Standard harvest control rules utilized in management of world fisheries almost uniformly use two control parameters-fishing mortality and spawning stock biomass. A control rule defines the target F and SSB and limit F and SSB reference points used to evaluate the status of the stock (Figure 3.7.1). Management actions should be taken when fishing mortality exceeds the F limit or spawning biomass falls below the biomass threshold. The SSB threshold is of particular importance as it guards against a population decline below a critically low value.

      It is a common practice to use a precautionary approach when choosing a target fishing mortality. This often involves adopting a value that is lower than the maximum sustainable value as a target to account for uncertainty in the estimate of maximum sustainable F. As the maximum sustainable F estimate grows more uncertain, the precautionary reduction in F used for management should also increase.

Candidate BRPS for Paddlefish.

      At the present time, there are no formally adopted target or limit reference points for management of Paddlefish stocks in the Mississippi River basin. We review several potential biological reference points with respect to their suitability for management of the commercial and recreational fisheries. In selecting candidate BRPs the following consideration were taken into account:

1. What BRPs can be estimated from the available data and assessment methods?

2. Are the candidate BRPs robust enough for use over the assessment period, and under changing environmental or anthropogenic conditions?

3. What objectives do the managers wish to achieve? Examples of management objectives are: to maintain stock levels at some level above a minimum historic catch or biomass level, to maintain fishing pressure at or below some historic or current level, or to maintain abundance at or above some fraction of the virgin abundance level (i.e. use a $B_{x\%}$ reference point).

Biomass reference points.

Currently, there are no biomass time-series estimates available for any Paddlefish stock at this moment, nor were we able to produce any in this analysis due to data limitations. In this respect, Paddlefish fisheries remain largely data-poor. If and when biomass estimates become available in the future, it would be highly desirable to develop biomass or SSB target and limit reference points for each stock being managed.

While absolute biomass estimates require either regular survey-based estimates or time-series of catch and age- or size-structure of the catch for use in formal stock assessment models, it may be possible to develop a relative index of abundance based on field sampling, such as gillnet catch per unit of effort (CPUE). In cases when CPUE measures are available for periods when the stock was considered to be in a healthy state and also when it was appeared to be at low abundance, those measurements could be used as empirical biomass reference points until absolute biomass estimates are developed. Such empirical target and limit indices of population biomass must be stock specific due to the fact that productivity of different stocks varies substantially.   In the absence of biomass reference points, the focus in the near-term future should be on selecting appropriate fishing mortality reference points.

Fishing mortality reference points

As mentioned above, the most frequently used reference points for fishing mortality targets and limits are F_{MSY} and its proxies, such as $F_{0.1}$, F_{max}, $F_{\% \ msp}$, F=M, F_{MER} and others. F_{MSY} is usually the most desirable reference point, defined as the value of F which produces the maximum yield over the long-term. Historically, this was

considered as a fishery target, but with the development of the precautionary approach, many management authorities adopted F_{MSY} as a limit reference point. For example, F_{MSY} is used as a limit reference point in US federal waters (EEZ) by all U.S. fishery management councils, as prescribed by the Magnuson-Stevens Fishery Conservation and Management Act. The F_{MSY} estimate is preferred because it integrates all elements defining population productivity, including growth, maturity, fecundity, as well as the relationship between stock size and recruitment. Unfortunately, because there are no time-series of recruitment and SSB estimates for any Paddlefish stock, we were unable to derive F_{MSY} directly by using a stock-recruitment relationship (e.g. using the Sissenwine and Shepherd (1987) method). In addition, the paucity of reliable catch estimates and indices of abundance with contrasting exploitation patterns for any stock prevented us from estimating F_{MSY} using surplus-production models. Situations in which no reliable statistics on landings and fishery dependent or fishery independent indices are available are not uncommon. In the absence of such information, proxy reference points are usually developed that are built on basic life-history information. There are several proxies for F_{MSY} that can be considered as alternatives.

F_{max} and $F_{0.1}$

With the introduction of the dynamic-pool model (Beverton and Holt, 1957), F_{max} was used extensively in the past as target or limit reference point. F_{max} was one of the earliest measures used as a proxy for F_{MSY}. However, it was often believed to be an overestimate of F_{MSY}, because it does not account for the fact that recruitment must decline at low spawning-stock abundances. Computer simulations have also demonstrated that F_{max} invariably overestimates F_{MSY} if a Beverton-Holt (1957) stock-recruitment relationship applies, although F_{MSY} can sometimes exceed F_{max} with a Ricker (1958) curve. For this reason, and taking into account economic considerations, $F_{0.1}$ was developed and promoted as a more prudent alternative (Gulland and Boerema, 1973). Although $F_{0.1}$ is commonly interpreted as a conservative or cautious estimate of F_{MSY}, this is not always the case (Mace, 1994; Mace and Sissenwine, 1993). And even when $F_{0.1}$ does underestimate F_{MSY}, the equilibrium yields associated with the two reference points may be relatively very close (based on the argument that the difference between the

equilibrium yields associated with F_{max} and $F_{0.1}$ are usually small, and F_{MSY} is usually less than F_{max}).

The YPR / SPR analysis completed in this study revealed that with very few exceptions, the yield-per-recruit curve has an asymptotic shape, with yield continuously increasing with an increase in fishing mortality. Lacking maximum values for yield and for egg (roe) production, the yield is maximized at the highest possible fishing mortality that still guarantees sustainable reproduction, Therefore, the limit on fishing mortality is defined by reproductive sustainability rather than by potential yield. The target and limit F reference points safeguarding the appropriately defined minimum level of spawning potential will effectively determine the level of the flesh or roe yield from the population. Hence, the F_{max} concept does not seem to be useful in the case of Paddlefish.

The $F_{0.1}$ introduced by Gulland and Boerema, (1973) as a more precautionary level of F is usually substantially lower than F_{max}, and at the same time achieves a yield only slightly lower than the yield at F_{max}. In the case of Paddlefish, the $F_{0.1}$ value had a tendency to exceed $F_{40\%}$ and $F_{30\%}$ for most of the stocks when low minimum sizes were in place, and thus should not be considered sufficiently safeguarding against overfishing. However, at a large minimum size limit, $F_{0.1}$ appears to be equal or lower than $F_{30\%}$ and $F_{40\%}$ values, thus equally or more conservative. Because the yield-per-recruit analyses do not account for stock – recruitment relationships, both F_{max} and $F_{0.1}$ are reference points in the context of growth overfishing, not recruitment overfishing. Since $F_{0.1}$ does not maximize yield, and does not offer quantitative estimate of reproductive potential, it does not offer any advantage compared to the F reference points based on the spawning potential. If $F_{0.1}$ is selected as a potential candidate reference point, it is advisable to estimate the corresponding percent SPR value and compare it to recommended limits for the SPR threshold (see SPR discussion below).

Natural mortality based F_{MSY} proxy.

The natural mortality rate (*M*) has often been considered to be a conservative estimate of F_{MSY}; however, it is becoming more frequently advocated as a target or limit for fisheries with a modest amount of information. In fact, in several fisheries, *F*=0.8*M and *F*=0.75*M have been suggested as default targets for data-poor cases (Thompson,

1993; Brodziak et al., 2011). Zhou et al., 2012 carried a meta-analysis on 245 fish species and linked F_{MSY} and $F_{\%MSP}$ to M. They found that natural mortality is the most important life history parameter affecting F_{MSY} and proposed to use their best model $F_{MSY} = 0.87M$ (standard deviation = 0.05) in data poor situations. This is very similar to Thompson's rule of $F \leq 0.8\,M$ and more conservative than $F = M$ (Francis, 1974). Natural mortality based F_{MSY} proxies clearly are more conservative (precautionary) than most of other alternatives ($F_{0.1}$, F_{MSY}, $F_{30\%}$, $F2_{0\%}$, F_{max}, F_{MER}) and more likely to prevent overfishing, but will also require the most significant reductions in commercial and recreational harvests if selected as a target or limit reference point.

$F_{\%MSP}$ reference points

Fishing mortality reference points, based on the percent of the maximum spawning potential (%MSP) of unfished population, gained strong acceptance everywhere in the world as proxies or independent measures of targets and limits when the F_{MSY} estimate was not available. MSP is the ratio between the number of eggs produced during a recruit's lifetime for a given fishing mortality divided by the number of eggs produced in the absence of fishing. As such, it measures the proportional reduction in total potential productivity attributable to fishing. If an appropriate %MSP reduction can be specified, the fishing mortality that achieves that MSP ($F_{\%MSP}$) can be calculated. This proxy for F_{MSY} currently forms the basis of F-based reference points to define overfishing and the corresponding spawning biomass, for many stocks in the world. The challenge for this type of reference point is specifying an appropriate %MSP; in a data-poor situation, such as Paddlefish stocks, that specification can be difficult.

The application of MSP-based reference points was initially focused on avoiding fishing rates that would lead to reductions in recruitment (recruitment overfishing; Myers et al., 1994). Values in the range $F_{20\%}$ to $F_{30\%}$ have frequently been used to characterize recruitment overfishing thresholds (Rosenberg et al., 1994), while values in the range $F_{30\%}$ to $F_{40\%}$ have been used as proxies for F_{MSY}. Mace and Sissenwine (1993) advocated $F_{20\%}$ as a recruitment overfishing threshold for well-known stocks with at least average resilience and $F_{30\%}$ as a recruitment overfishing threshold for less well-known stocks or those believed to have low resilience. Mace (1994) expanded the earlier analysis and suggested

$F_{40\%}$ as a default F_{msy} proxy when the stock–recruit relationship is unknown. Clark (1991) evaluated Alaskan groundfish stocks through extensive simulation, and recommended $F_{35\%}$ as an appropriate proxy for F_{MSY}. Clark (1993) revisited his first analysis (Clark, 1991) by incorporating recruitment variability, and revised his recommended F_{MSY} proxy to $F_{40\%}$. More recently, Clark (2002) concluded that an $SPR_{40\%}$ should meet current management needs but noted that for species with low resiliencies the appropriate fishing level could be $F_{60\%}$ or even $F_{70\%}$ (Clark, 2002). Brooks et al. (2010) investigated the relationship between MSP, maximum recruitment production, and F_{MSY} and indicated that only the most resilient stocks would not exceed F_{MSY} when using a reference point based on 30% MSP. Very long-lived, slow-maturing species would require much higher levels of MSP to ensure that $F < F_{MSY}$. For those species, an MSP of at least 60% would be required, and because $MSP_{MSY} < MSP_{MER}$, the appropriate MSP level could be higher if management focuses on yield in biomass (or roe in case of Paddlefish) rather than in number. We demonstrated this analytically.

Suggested reference points for Paddlefish

Due to the lack of direct estimates of F_{MSY} for any Paddlefish stock, proxy estimates must be used. Fishing mortality reference points based on the percent of the maximum spawning potential (%MSP) of unfished population appears to be the most suitable set of reference points because they account for major processes, including growth, mortality, maturity, fecundity, and fishing selectivity. The range of %MSP that provides sustainable reproduction and approximates MSY requirements has been investigated in the literature for a large number of data-rich species with various life-histories and taxonomic orders. As discussed above, the proposed limit (threshold) for MSP reduction is often in the range of 30 to 40%, while MSPs of 40 % or higher were shown to often be a proxy to F_{MSY}. Basic life-history parameters such as greater longevity and low natural mortality, relatively slow maturation, and a long life-period after reaching near maximum size, suggest that Paddlefish are not likely to be among the most resilient species, so it would be reasonable to choose an upper limit of the range. An $F_{\%MSP}$ in the range of $F_{30\%}$ to $F_{40\%}$ should be considered as limit reference point, until direct estimates of F_{msy} (or other reference point that directly describes the objectives of

management) become available. The target $F_{\%MSP}$ can be selected as a fraction of the limit. This range of $F_{\%spr}$ values is currently being used by many fisheries management bodies for species with similar life-histories in data limited situations. For example, $F_{40\%}$ is used extensively as a limit reference point by the New England Fishery Management Council to manage groundfish species of the Northwest Atlantic, while $F_{35\%}$, $F_{40\%}$ and $B_{40\%}$ were adopted as limit reference points for many species by the North Pacific Fishery Council.

When facing significant uncertainty in the definition of reference points, as is the case for the Paddlefish, caution is required. The Precautionary Principle, proposed by FAO in the Conduct Code for Responsible Fisheries (FAO, 1995), declares that the limitations, uncertainties, or lack of data for the assessment or for the estimation of parameters, cannot serve as a justification for not applying regulatory measures, especially when there is information that the stocks are over-exploited. The uncertainties associated with the estimation of F_{lim}, and B_{lim}, therefore require selecting more conservative reference points to reduce the chances of overfishing due to misspecification of limit reference points. The assumptions and the consequences of adopting alternative hypotheses about the stock and fishing characteristics should always be considered to justify the choice. With these considerations in mind, a natural mortality based reference point such as $F_{lim} = 0.87M$ would certainly provide more protection to the population, but might be difficult to achieve immediately due to required cuts in the harvest. However, if this option can be applied to certain stocks, it should be encouraged. The population response in such cases could be compared with other stocks and provide valuable information on stock resilience, helping to better guide management in the future. It appears that selecting $F_{30\%}$ or $F_{40\%}$ as a limit reference point is a reasonable initial step towards the development of reference points for Paddlefish stocks. The target F reference point can be selected as a fraction of the F limit to ensure that the limit is not exceeded due to scientific and management uncertainty. Because the percent MSP reduction can be achieved with multiple combinations of management measures, the actual values for F reference points may vary substantially due to the choice of minimum legal size, fishing seasons, bag limits, etc. Actual values will vary among stocks as well and stock specific

estimates are recommended that will account for regional differences in major population processes such as growth, maturity, fecundity, mortality.

3.8. Comparison of Mortality Rates to Reference Points

We compared estimated fishing mortality rates to estimated reference points by subtracting an assumed value for the natural mortality rate from the estimated total mortality rates from Section 2.10. We then calculated the ratio of estimated fishing mortality rate relative to the $F_{40\%}$ proposed target using reference points from the nearest system in the region and the minimum size regulation for the system: Reference points and mortality estimates were available for Lake Francis Case and systems on the Arkansas River; for systems in Tennessee we used reference points from Lake Kentucky; for systems in Mississippi, we used reference point estimates from the Alabama River; we compared reference point estimates for the Mississippi River with mortality rate estimates from the Mississippi River in Mississippi, Arkansas, Tennessee, and Missouri.

In almost all of the systems the total mortality rates appeared to be high relative to the natural mortality rates (Table 3.8.1). For Lake Francis Case, the estimated target fishing mortality rate was 0.05-0.06 (for $F_{40\%}$). If we subtract assumed natural mortality from the total mortality, fishing mortality for this system is estimated at about 0.11, almost twice the $F_{40\%}$ value. For the Arkansas River pools, the estimated total mortality rate was 1.35 and estimated F was 1.21, nearly six times higher than $F_{40\%}$, 0.21. Fishing mortality appeared to substantially exceed $F_{40\%}$ in the Tennessee systems, with ratios of estimated fishing mortality to $F_{40\%}$ between 1.8 and 8.4. In Mississippi, the ratios of estimated fishing mortality rates relative to the targets were somewhat lower, between 0.5 and 4.41, but the lower estimates are mostly a function of the high natural mortality rate estimates used. Estimates of fishing mortality from the Mississippi River were all substantially higher $F_{40\%}$, ranging from 2.7 in Arkansas in Missouri to 8.4 in Tennessee.

4. Recommendations

4.1. Management Recommendations

Develop Objectives for Management

Without objectives it is impossible to determine whether management is successful or not. We recommend development and adoption of long-term fishery management objectives. An example of a broad general objective is to maximize the use of population productivity in the form of optimum yield for commercial fishery and maximize enjoyment for recreational fishery.

Adopt Fishing Mortality Rate Reference Points

Currently, no states use biological reference points to manage their fisheries, and exploitation or mortality rates are not estimated annually in most regions to compare with reference points. Without this kind of framework, it is very difficult to determine if fisheries are being sustainably managed. Biological reference points should be developed for all commercially and recreationally important Paddlefish stocks. At the first stage, fishing mortality targets and thresholds should be established. When absolute or relative estimates of spawning stock biomass become available, biomass reference points should be established as well. We recommend that states adopt biological reference points for target and limit fishing mortality rates, perhaps based on the analyses described in Section 3. We recommend SPR-based reference points $F_{30\%}$ and $F_{40\%}$ as limit and target reference points. The evaluation of the biological reference points should be completed in few years after their implementation to ensure their appropriateness.

Adopt Precautionary Management in the Face of Uncertainty

The Precautionary Approach should be considered by management with regard to the choice of reference points and formulation of the regulation measures. For stocks where regular age data collection is not possible due to resources constraints, more conservative size and season restrictions are necessary. Management tools that can be considered include limitation of the number of fishing licenses, limitation of the total fishing effort each year (limiting fishing days, number of trips, number

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of days at sea, etc, limitation of Total Allowable Catch (TAC) , minimum size (or weight) of the landed individuals, minimum mesh size, season and area.

Estimate Fishing Mortality Rates

We recommend development of relatively low cost methods for estimating fishing mortality rates. For Paddlefish, the most cost effective approaches likely involve implementation of well-coordinated tagging studies. For example, on many systems a short term mark recapture study could be implemented where fish were marked with conventional tags during one week and recaptures are collected the next week. Population estimates would be calculated using the Lincoln-Peterson estimator, and exploitation rates could be calculated by dividing the catch by the estimated population size. This approach would require two weeks of staff and boat time per system in which it is implemented. A similar approach is used for estimating walleye population size and exploitation rates in Wisconsin treaty lakes. Concerns with this approach are that any unreported harvest or bycatch mortality will not be incorporated in the estimated exploitation rate. Alternatively, use of acoustic tags with tagging arrays throughout the fishing areas could allow one to estimate total fishing mortality including unreported fishing and bycatch (catch and release). The methods for analyzing these types of data sets are more complicated than a simple conventional tagging study, but they have been developed by Hightower and colleagues. Recently, such a study was conducted by Oklahoma for other purposes, but the data could be used to estimate exploitation rates.

Other options are also available. Martell and Walters (2002) described a low cost method of estimating exploitation rates. The approach can be implemented by tagging fish before the fishing season. The catch is then monitored for recoveries of tagged individuals. This approach can be implemented either by monitoring the total catch, which will provide the most precise estimates, or by monitoring a known proportion of the catch. This method of monitoring the fishery provides estimates of exploitation rate by size class. However, if females are targeted, this will mean that the exploitation rate will be underestimated for males and overestimated for females. If abundance estimates are desired, one must make assumptions about natural mortality and immigration/emigration and monitor the number of unmarked fish in the harvest.

This type of study has many of the same limitations of other mark-recapture studies, such as bias caused by release mortality, unaccounted tag shedding and non-reporting of tags. The simple version of the approach only estimates the exploitation rate of retained fish. If release mortality rates

are moderate to high and a substantial fraction of the catch is released, this approach will not fully quantify the effect of the fishery on the population. Estimates of tag retention can be obtained by double tagging a portion of the marked fish and determining the proportion of fish that retained both tags compared to the proportion that only retain one tag (e.g., Fabrizio et al. 1999). Another common source of bias in mark-recapture studies is a reporting (or detection) rate of tags less than 100%. One way to estimate the reporting rate is to plant tagged fish in the processing facilities to determine the proportion of tags that are recovered and reported.

In some systems, data are available for full age-structured stock assessments (e.g. Lake Sakagawea and Yellowstone Lake). In these systems we recommend application of a full age-sex structured statistical stock assessment such as the one applied for yellow perch in southern Lake Michigan (Wilberg et al. 2005). These types of statistical models are a substantial advance over the older virtual population type assessment methods that have been applied to Paddlefish (Scarnecchia et al. 2013).

Develop Harvest Control Rules

There are generally three types of harvest control rules available to manage fisheries: constant escapement, constant fishing mortality rate, and constant catch (Deroba and Bence 2008). Harvest control rules prescribe management actions to be taken when fishing mortality exceeds either the target or the limit reference points. The goal of constant escapement harvest policies is to allow a fixed number of adults to spawn each year; the remainder of the population is then harvested. These types of control rules are generally not used for many fisheries because, while they protect the stock at low abundance, they cause closures of the fishery at low abundance and high interannual variability in the catch. They have primarily been used for Pacific salmon populations. Constant catch control rules aim to always harvest a constant number or biomass of fish from the population. While these types of control rules are often appealing to stakeholders, the overall catch has to be set at a fairly low level to avoid overfishing during population declines because fishing mortality increases as abundance decreases with this control rule. Lastly, most fisheries in the world that use a control rule to specify harvest targets use some form of constant fishing mortality control rule. Constant fishing mortality control rules specify that a constant fraction of the population be caught each year. They are flexible for the definition of population size (e.g., adult abundance, female spawning stock biomass, etc.), and can also specify a conditional mortality rate such that the target fishing mortality rate depends on the

stock size. Constant fishing mortality rate control rules often provide a balance between relatively stable and high catch when the stock is in good condition, but protection for the stock, because catches decrease with stock size, as abundance decreases.

Improve Data Collection

Efforts should be made to provide reliable annual estimates of catch, fishing effort, catch age and size structure and fishery dependent and fishery independent indices wherever possible.

4.2. Research Recommendations

Conduct aging validation studies using stocked fish of known age

Accurate age data are required for many of the approaches used to estimate mortality rates, abundance, growth, and recruitment (Quinn and Deriso 1999). Studies have been done to evaluate the accuracy of ages by comparing the precision of ages (multiple reads of the same structure), the consistency with tagging data (i.e., is the fish older than the time at large), and accuracy of aging known age fish. The first two approaches cannot quantify the accuracy of ages, and the third approach has only been done on relatively small sample sizes of relatively young fish. In those cases it may show some signs of a negative bias in age beginning at ages 8-10. Additionally, accuracy of ages may differ among research groups and among growth conditions experienced in different regions. Data from known-age fish that were stocked can be used to test the accuracy of aging.

Continued development of the MICRA database

The MICRA tagging database contains a wealth of information. However, its utility could be improved. Maintaining a high quality database requires a substantial continued investment. One of the primary areas that is required is quality assurance/quality control. The MICRA tagging database has many errors and incomplete entries. For example, names of basins and locations do not follow consistent entry, and there are quite a few size observations that are implausibly large or small. Data entered into the MICRA tagging database needs to undergo at least one quality control check.

Additionally, more complete metadata descriptions would be helpful. Lastly, increasing the number of states that participate in the database would be useful. If the data are used routinely approaches can be developed to improve the quality of the data.

Conduct In-depth Stock Assessments

At least two stocks appear to have sufficient data accumulated to implement modern age structured assessment methods, such as statistical catch at age analysis.

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6. Tables

Table 2.2.1. Total number of movements and number of coded-wire tagged (CWT) wild-origin Paddlefish obtained from the MICRA database by state postal abbreviation. Intrastate movements (marked and recaptured in the same state) are listed on the diagonal with the top number indicating the number of recaptures and the bottom number indicating the total number of Paddlefish CWT by a state. Interstate movements (marked in one state and recaptured in a different state) are listed on the off-diagonal where fish were tagged in the state listed in the row and recaptured in the state listed in the column. Light-gray, outlined boxes indicate movement between adjacent states within a basin; medium-gray boxes indicate movement between nonadjacent states within a basin; and black boxes indicate movement between basins. Table adopted from Table 3 of Pracheil et al., 2012.

	AR	IL*	IN*	IA†	KS†	KY*	LA†	MN‡	MS*	MO*	NE†	OH‡	OK†	PA‡	SD†	TN*	TX‡	WV‡	WI‡
AR	4 / 31																		
IL*		190 / 5,446	6			28				3	3				3	1			
IN*		10	130 / 2,415			30							10		1				
IA†				138 / 2,938							2				8				
KS†					0 / 63														
KY*	6		37			59 / 2,578							1		1				
LA†							14 / 682												
MN‡			1					0 / 35											
MS*						1			0 / 120										
MO*						1				6 / 242									
NE†				4						3	172 / 3,513				339				
OH‡			11			7						39 / 489							
OK†													0 / 74						
PA‡														2 / 3					
SD†	3		3			1				4	110				247 / 2,717				
TN*						1				1						9 / 406			
TX‡																	1 / 29		
WV‡						1							1					0 / 55	
WI‡			2																0 / 395

* State allowing commercial and sport paddlefish harvest
† State allowing paddlefish sport harvest
‡ State with paddlefish harvest prohibited

Table 2.5.1. Mean length (EFL), standard deviation and coefficient of variation for Kentucky Lake Paddlefish.

age	sex	mean EFL	st dev	CV
3	M	632.00	NA	NA
4	M	700.57	83.56	0.12
5	M	804.13	53.88	0.07
6	M	813.10	49.44	0.06
7	M	837.29	41.73	0.05
8	M	889.15	35.50	0.04
9	M	866.38	27.78	0.03
10	M	884.00	2.16	0.00
3	F	542.00	35.00	0.06
4	F	645.57	49.44	0.08
5	F	705.09	63.86	0.09
6	F	812.34	43.56	0.05
7	F	864.04	66.46	0.08
8	F	926.05	53.51	0.06
9	F	976.74	48.26	0.05
10	F	979.82	48.40	0.05
11	F	1065.00	52.33	0.05

Table 2.5.2. Mean length (EFL), standard deviation and coefficient of variation for Lower Missisippi River Paddlefish (data from Tripp et al., 2012).

age	sex	mean EFL	st dev	CV	sex	mean EFL	st dev	CV
7	M	807.72	53.77	0.07				
8	M	823.69	44.86	0.05				
9	M	839.58	46.46	0.06	F	912.28	46.81	0.05
10	M	871.22	40.29	0.05	F	861.48	53.98	0.06
11	M	890.83	31.77	0.04	F	912.73	58.50	0.06
12	M	902.15	45.76	0.05	F	925.51	46.33	0.05
13	M	924.98	41.38	0.04	F	958.53	43.04	0.04
14	M	935.83	49.41	0.05	F	988.06	51.01	0.05
15	M	1016.00	71.84	0.07	F	1031.24	24.01	0.02
16	M	NA	NA		F	1028.70	55.36	0.05
17	M	996.95	NA		F	1035.05	NA	
18	M	946.15	NA					
19	M	NA	NA		F	1054.10	NA	
20	M	1143.00	NA					
			average CV	0.05			average CV	0.05

Table 2.5.3. Mean length (EFL), standard deviation and coefficient of variation for Arkansas River female Paddlefish, pools combined (data from Leone et al., 2012).

age	sex	mean EFL	st dev	CV
4	F	581.5	33.2	0.06
5	F	734.5	135.1	0.18
6	F	693.5	62.9	0.09
7	F	858.8	44.7	0.05
8	F	870.2	84.2	0.10
9	F	930.7	69.3	0.07
10	F	952.5	51.6	0.05
11	F	970.0	48.9	0.05
12	F	971.6	38.2	0.04
13	F	990.2	37.0	0.04
14	F	979.3	37.9	0.04
15	F	1012.0	55.2	0.05
16	F	983.0	NA	NA
			average CV =	0.07

Table 2.5.4. Mean length (EFL), standard deviation and coefficient of variation for Lower Mississippi River (data from Risley, 2012).

age	sex	mean EFL	st dev	CV	sex	mean EFL	st dev	CV
3	F	435	25.46	0.06	M	447	17.40	0.04
4	F	550	22.3	0.04	M	547	11.3	0.02
5	F	617	46.7	0.08	M	604	48.1	0.08
6	F	678	52.3	0.08	M	678	39.6	0.06
7	F	704	50.4	0.07	M	735	42.0	0.06
8	F	806	54.9	0.07	M	783	42.5	0.05
9	F	826	56.2	0.07	M	816	45.3	0.06
10	F	872	47.5	0.05	M	833	35.5	0.04
11	F	898	39.7	0.04	M	849	53.2	0.06
12	F	920	40.2	0.04	M	875	60.6	0.07
13	F	933	56.5	0.06	M	897	38.2	0.04
14	F	957	55.6	0.06	M	963	10.6	0.01
15	F	981	29.4	0.03	M	929	11.3	0.01
16	F	995	43.2	0.04	M	927		
17	F	985	38.2	0.04	M	924		
18	F	1003	42.9	0.04				
19	F	1022	18.4	0.02				
20	F	1017	1.4	0.00				
21	F	1020						
22	F	1029						
23	F	1040						
24	F	1095						
			average CV =	0.05			average CV =	0.05

Table 2.5.5. Von Bertalanffy growth parameters estimates by region and sex.

citation	time frame	State	Water body	Sex	t0	K	Linf
Adams 1942	1942	Illinois	Illinois River	Both	0.06	0.35	115.84
Berg 1981		Montana	Lake Fort Peck	Both	NA	NA	136.70
Bronte & Johnson 1985	1980-1981	Kentucky/Tennessee	Lake Barkley	M	-0.177	0.2	96.70
Bronte & Johnson 1985	1980-1981	Kentucky/Tennessee	Lake Barkley	F	-0.217	0.153	116.30
Bronte & Johnson 1985	1980-1981	Kentucky/Tennessee	Kentucky Lake	M	-0.355	0.146	111.10
Bronte & Johnson 1985	1980-1981	Kentucky/Tennessee	Kentucky Lake	F	-0.534	0.134	112.40
Combs 1982	1979-1980	Oklahoma	Grand Lake and Neosho River	Both	2.85203	0.0995	146.9111
Hoffnagle & Timmons 1989	1985-1986	Kentucky/Tennessee	Kentucky Lake	Both	0.67583	0.1127	113.0411
Hoxmeier & Devries 1997	1994-1995	Alabama	lower Alabama River	Both	0.0667	0.117	127.60
Lein & Devries 1998	1992-1993	Alabama	Tallapoosa River	M	0.3374	0.149	110.00
Lein & Devries 1998	1992-1993	Alabama	Tallapoosa River	F	0.2761	0.181	110.50
Lein & Devries 1998	1992-1995	Alabama	Claiborne lock	Both	0.0895	0.229	106.70
Lein & Devries 1998	1992-1994	Alabama	Cahaba River	Both	0.1545	0.211	102.80
O'Keefe and Jackson 2009	2004-2005	Alabama	Demopolis Lake	M	0.0696	0.2844	97.18
Pasch et al. 1980	1975-76	Tennessee	Old Hickory Reservoir	Both	NA	NA	123.10
Paukert and Fisher 2001	1996-1998	Oklahoma	Keystone Reservoir	Both	0.12646	0.4312	105.7557
Pierce et al, 2011	2008-2009	South Dakota	Lake Francis	Both	-1.68	0.10	132.50
Pierce et al, 2011	2008-2009	South Dakota	Lake Francis	F	1.19	0.16	130.10
Pierce et al, 2011	2008-2009	South Dakota	Lake Francis	M	-2.59	0.10	118.90
Pitman 1991		Missouri	Table Rock	Both	NA	NA	130.10
Pitman 1991		Missouri	Lake of the Ozarks	Both	NA	NA	126.30
Reed et al. 1992	1987-1991	Louisiana	Lake Pontchartrain	Both	-0.71	0.276	120.50
Reed et al. 1992	1987-1990	Louisiana	Lake Henderson	Both	-0.731	0.303	102.80
Reed et al. 1992	1987-1989	Louisiana	Atchafalaya River	Both	-1.019	0.254	110.20

Table 2.5.5. continues..

citation	time frame	State	Water body	Sex	t0	K	Linf
Rosen et al. 1982	1972-1979	Nebraska/South Dakota	Missouri River	M	-5.159	0.133	84.90
Rosen et al. 1982	1972-1979	Nebraska/South Dakota	Missouri River	F	-2.215	0.17	90.30
Scarnecchia et al. 1996		North Dakota	Lake Sakakawea	Both	NA	NA	102.80
Scarnecchia et al. 2011	2008-2010	Oklahoma	Grand Lake	M	NA	0.3303	96.38
Scarnecchia et al. 2011	2008-2010	Oklahoma	Grand Lake	M	0.5285	0.3026	96.82
Scarnecchia et al. 2011	2008-2010	Oklahoma	Grand Lake	F	NA	0.2298	112.30
Scarnecchia et al. 2011	2008-2010	Oklahoma	Grand Lake	F	10.774	0.0676	133.60
This study	2010	Oklahoma	Grand Lake	F	4.1346	0.2305	105.91
This study	1991- 2010	Oklahoma	Grand Lake+ MOCRA data	F	-1.82	0.2016	110.92
Scarnecchia et al 2008 mgmt plan	2003	N Dakota	Sakakawea Lake	F	2.1451	0.1022	124.6
Scarnecchia et al 2008 mgmt plan	2003	N Dakota	Sakakawea Lake	M	5.2882	0.1127	101.10
Scarnecchia et al 2008 mgmt plan	2003	Montana	Yellowstone R	F	3.2195	0.1149	118.40
Scarnecchia et al 2008 mgmt plan	2003	Montana	Yellowstone R	M	0.1597	0.1864	99.15
Scholten & Bettoli 2005	2003-2004	Kentucky/Tennessee	Kentucky Lake	Both	-1.53	0.13	127.90
Scholten & Bettoli 2005	2003-2004	Kentucky/Tennessee	Kentucky Lake	M	-1.08	0.34	90.17
Scholten & Bettoli 2005	2003-2004	Kentucky/Tennessee	Kentucky Lake	F	-0.91	0.14	129.99
Scholten reestimated	2003-2004	Kentucky/Tennessee	Kentucky Lake	Both	-0.77	0.228	1035
Scholten reestimated	2003-2004	Kentucky/Tennessee	Kentucky Lake	M	-0.43	0.385	895.3
Scholten reestimated	2003-2004	Kentucky/Tennessee	Kentucky Lake	F	-0.32	0.176	1202.3
Leone et al. 2011	2003-2005	Arkansas	Dardanelle lake	F	-0.328	0.185	110.50
Leone et al. 2011	2003-2006	Arkansas	Ozark Lake	F	-0.329	0.2	104.50
Leone et al. 2011	2003-2007	Arkansas	Pool 13	F	-0.359	0.177	106.50
Leone et al. 2011	2003-2005	Arkansas	All combined	F	-1.115	0.132	117.80

Table 2.5.5. continues..

citation	time frame	State	Water body	Sex	t0	K	Linf
Leone et al. 2011	2003-2006	Arkansas	Ozark Lake	M	-0.417	0.211	99.30
Leone et al. 2011	2003-2007	Arkansas	Pool 13	M	-0.255	0.249	91.60
Risely, 2012	2008-2010	Arkansas	Lower Mississippi	both	-0.995	0.135	108.2
Risely, 2012	2008-2010	Arkansas	Lower Mississippi	M	-0.650	0.170	99.000
Risely, 2012	2008-2010	Arkansas	Lower Mississippi	F	-0.940	0.140	108.300
Risely, 2012		Arkansas	Lower Mississippi	M	-0.280	0.184	98.797
Tripp et all, 2012	2011	Arkansas/Mississippi	Mississippi	both	-2.649	0.13	113.2
Tripp et all, 2012	2011	Missouri/Kentucky	Mississippi	both	-4.334	0.1	113.4
Tripp et all, 2012	2011	pooled	Mississippi	both	-4.383	0.094	118.5
This study	1991-2012	MICRA states	Gulf Basin	both	1.06859	0.4865	97.73
This study	1991-2012	MICRA states	Mississippi Basin	both	0.58258	0.6029	98.97
This study	1991-2012	MICRA states	Missouri Basin	both	2.03046	0.2348	94.47
This study	1991-2012	MICRA states	Ohio Basin	both	0.70139	0.4233	101.52

Table 2.5.6. Basin level parameter estimates and asymptotic standard errors (SEs) for the age-based von Bertalanffy growth model for Paddlefish.

Basin	Estimates			SEs		
	Linf	K	t0	Linf	K	t0
GULF	1073	0.345	-1.71	19.2	0.131	1.17
MISSISSIPPI	1073	0.298	-1.33	19.2	0.757	1.18
MISSOURI	1073	0.161	-3.11	19.2	0.691	1.34
OHIO	1073	0.303	-1.66	19.2	0.786	0.94
log_K_basin_sigma	-2.36	0.69				
log_t0_basin_sigma	-0.10	0.78				
log_Linf_site_sigma	4.22	0.22				
log_K_site_sigma	-1.95	0.25				
log_t0_site_sigma	0.84	0.27				

Table 2.5.7. Reach level parameter estimates and asymptotic standard errors (SEs) for the age-based von Bertalanffy growth model for Paddlefish. Reaches with known ages from hatchery releases are in all capital letters and reaches with read ages from structures are in lower case.

Basin	Reach	n	Estimates L_∞	K	t0	SE L_∞	K	t0
Gulf	RED-	16	1075.5	0.32	-1.18	60.51	0.17	1.83
Gulf	RED-LAKE TEXOMA	547	949.0	0.55	-1.01	31.01	0.17	1.60
Gulf	WASHITA-LAKE TEXOMA	52	1118.0	0.39	-0.50	46.99	0.17	1.62
Mississippi	-	64	1072.3	0.29	-0.71	70.98	0.18	1.64
Mississippi	ARKANSAS-KAW LAKE	59	1136.8	0.40	-0.58	36.54	0.12	1.62
Mississippi	VERDIGRIS-OOLAGAH	328	1041.3	0.54	-0.66	28.49	0.12	1.62
Mississippi	WHITE-TABLE ROCK LAKE	521	1078.9	0.22	-1.52	33.04	0.12	1.62
Mississippi	Lake Dardanelle	107	1031.6	0.24	0.26	44.58	0.13	1.81
Mississippi	Lake of the Ozarks	227	971.8	0.33	0.72	31.90	0.14	1.88
Mississippi	Pool 13 (Arkansas)	210	1029.1	0.17	-1.94	46.56	0.12	2.01
Missouri	MISSOURI-FORT RANDALL DAM TAILWATERS	174	1055.6	0.08	-6.21	52.48	0.11	2.17
Missouri	MISSOURI-BELOW GAVINS POINT DAM	456	1023.8	0.08	-11.70	47.81	0.11	2.72
Missouri	MISSOURI-LAKE FRANCIS CASECASE	398	1140.0	0.14	-2.91	40.76	0.11	1.66
Missouri	MISSOURI-LEWIS AND CLARK LAKE	190	1063.3	0.11	-3.64	70.26	0.12	1.89
Missouri	OSAGE-BAGNELL DAM	23	1103.3	0.16	-1.97	62.67	0.11	1.76
Missouri	OSAGE-HARRY S TRUMAN LAKE	168	1130.1	0.18	-1.81	39.09	0.11	1.65
Missouri	OSAGE-LAKE OF THE OZARKS	76	1070.5	0.18	-1.91	50.92	0.11	1.66
Missouri	REPUBLICAN-	13	1068.9	0.22	-2.81	62.20	0.12	1.94
Missouri	WHITE-	75	1155.1	0.12	-2.27	52.75	0.11	1.74
Missouri	WHITE-LAKE FRANCIS CASECASE	42	1144.8	0.13	-2.69	53.35	0.11	1.92
Ohio	ALLEGHENY-KINZUA	14	1161.3	0.55	-0.35	59.50	0.15	1.62
Ohio	HOLSTON-CHEROKEE RESERVOIR	10	1064.7	0.26	-0.98	58.98	0.15	1.63
Ohio	Kentucky Lake	576	1042.6	0.22	-0.88	42.48	0.14	1.68

Table 2.5.8. Parameter estimates from the growth increment von Bertalanffy model. Locations are indicated by the basin and reach. Parameters are presented with their standard errors (SE). The last three rows provide the standard deviation estimates for the random effects (on the natural log scale).

Basin	Reach	Linf	SE	K	SE
Gulf	BAYOU NEZPIQUE	909.1	65.1	0.476	0.072
Gulf	MERMENTAU-POOL 1	848.3	43.4	0.476	0.072
Gulf	MERMENTAU-LAKE ARTHUR	935.0	45.4	0.476	0.072
Gulf	RED-LAKE TEXOMA	1006.9	31.7	0.476	0.072
Mississippi	ARKANSAS-KAW LAKE	1102.1	34.1	0.375	0.069
Mississippi	BLACK	878.6	60.2	0.375	0.069
Mississippi	BLACK-8	925.8	82.9	0.375	0.069
Mississippi	CEDAR	949.2	96.1	0.375	0.069
Mississippi	DESMOINES	961.6	80.5	0.375	0.069
Mississippi	ILLINOIS-ALTON	913.0	46.3	0.375	0.069
Mississippi	MISSISSIPPI-12	978.5	77.8	0.375	0.069
Mississippi	MISSISSIPPI-13	925.0	29.8	0.375	0.069
Mississippi	MISSISSIPPI-14	914.9	34.4	0.375	0.069
Mississippi	MISSISSIPPI-26	884.5	32.8	0.375	0.069
Mississippi	MISSISSIPPI-27	1004.4	74.6	0.375	0.069
Mississippi	MISSISSIPPI-5A	938.3	80.4	0.375	0.069
Mississippi	VERDIGRIS-OOLAGAH	1090.8	28.1	0.375	0.069
Mississippi	WHITE-TABLE ROCK LAKE	1001.8	27.1	0.375	0.069
Missouri	BIG SIOUX	902.6	51.1	0.228	0.069
Missouri	BLUE	1084.0	100.4	0.228	0.069
Missouri	MISSOURI	930.6	68.4	0.228	0.069
Missouri	BELOW GAVINS POINT DAM	875.6	27.7	0.228	0.069
Missouri	LAKE FRANCIS CASECASE	953.9	27.4	0.228	0.069
Missouri	LEWIS AND CLARK LAKE	888.0	30.1	0.228	0.069
Missouri	NIANGUA-LAKE OF THE OZARKS	963.7	68.8	0.228	0.069
Missouri	HARRY S TRUMAN LAKE	1085.7	30.0	0.228	0.069
Missouri	OSAGE-LAKE OF THE OZARKS	996.5	31.7	0.228	0.069
Missouri	WHITE	955.1	74.5	0.228	0.069
Missouri	WHITE-TABLE ROCK LAKE	996.0	41.6	0.228	0.069
Ohio	ALLEGHENY-KINZUA	1318.7	78.8	0.350	0.074
Ohio	CUMBERLAND-BARKLEY	955.8	75.9	0.350	0.074
Ohio	GREAT MIAMI-MARKLAND	921.1	41.7	0.350	0.074
Ohio	CHEROKEE RESERVOIR	1028.7	41.3	0.350	0.074
Ohio	OHIO-BELLEVILLE	926.3	60.2	0.350	0.074
Ohio	OHIO-CANNELTON	876.0	56.9	0.350	0.074
Ohio	OHIO-MARKLAND	917.8	42.0	0.350	0.074
Ohio	OHIO-MYERS	948.4	30.3	0.350	0.074
Ohio	OHIO-NEWBURGH	893.1	59.5	0.350	0.074
Ohio	OHIO-RACINE	967.5	103.8	0.350	0.074
Ohio	OHIO-SMITHLAND	891.5	35.5	0.350	0.074
Ohio	SOUTH CROSS CREEK	966.4	97.5	0.350	0.074
Ohio	WABASH	768.5	31.1	0.350	0.074
	log_Linf_basin_sigma	-4.45	1233.8		
	log_K_basin_sigma	-2.39	0.375		
	log_Linf_site_sigma	4.63	0.156		

Table 2.6.1. Length – weight relationship parameters.

Source	Water body	Sex	Length weight equation	weigth unit	length unit
Rosen et al. 1982	Missour River	Both	$\ln(W)=2.77*\ln(L)-10.14$	kg	cm
Combs,1982	Neosho River	both	$\log_{10}(W)=3.335*\log_{10}(L)-5.7542$	g	mm
Scholten & Bettoli 2005	Kentucky Lake	Both	$\log_{10}(W)=3.307*\log_{10}(L)-5.711$	g	mm
Scholten & Bettoli 2005	Kentucky Lake	M	$\log_{10}(W)=2.543*\log_{10}(L)-6.2353$	kg	mm
Scholten & Bettoli 2005	Kentucky Lake	F	$\log_{10}(W)=3.327*\log_{10}(L)-8.7243$	kg	mm
Hageman et al. 1985	Cumberlaand Lake	M	LoglOWkg = -3.79 + 2.65 LoglO EFLcm		
Hageman et al. 1986	Cumberlaand Lake	F	LOglOWkg = -5.09 + 3.09 LoglOEFLcm		
Hageman et al. 1987	Cumberlaand Lake	Both	LoglOWkg = -4.85 + 3.01 LoglOEFLcm '		
scharnechhia 2008	Lake Sakakawea	F	$W=0.000029L^{2.90}$	kg	cm
scharnechhia 2008	Lake Sakakawea	M	$W=0.00000829L^{3.116}$	kg	cm
scharnechhia 2008	Yellowstone River	F	$W=0.000004606L^{3.2868}$	kg	cm
scharnechhia 2008	Yellowstone River	M	$W=0.000033L^{2.8066}$	kg	cm
Bronte & Johnson 1985	Lake Barkley	M	$\ln(W)=2.822*\ln(L)-4.240$	g	cm
Bronte & Johnson 1985	Lake Barkley	F	$\ln(W)=3.100*\ln(L)-5.020$	g	cm
Bronte & Johnson 1985	Kentucky Lake	M	$\log(W)=3.197*\log(L)-5.329$	g	cm
Bronte & Johnson 1985	Kentucky Lake	F	$\log(W)=3.534*\log(L)-6.308$	g	cm
Genderke 1978	Upper Mississippi	F, ages 1-4	$\log10(W)= -6.44 + 3.38 \log10(FL)$		
Genderke 1978	Upper Mississippi	F, ages 11-18	$\log10(W)= -3.71 + 2.54 \log10(FL)$		
Genderke 1978	Upper Mississippi	M, ages 5-10	$\log10(W)= -8.03 + 3.92 \log10(FL)$		
This study based on Gordon, 2010	Grand Lake	F	$W= 7.112e-9EFL^{3.1198}$		
This study based on Gordon, 2010	Grand Lake	M	$W = 6.43E-09EFL^{3.1257}$		
Reed et al. 1992	Lake Henderson	Both	$\log_{10}(W)=2.51*\log_{10}(L)-6.34$		
Reed et al. 1992	Atchafalaya River	Both	$\log_{10}(W)=2.85*\log_{10}(L)-7.43$		
Reed et al. 1992	Lake Pontchartrain	Both	$\log_{10}(W)=3.46*\log_{10}(L)-9.17$		

Rider et al, 2011	Alabama River	both	Log10 (W) = 2.934 Log10 (L)-4.723	kg	mm
Leone et al, 2012	Lake Dardanelle	F	$\log_{10}(W)=3.423*\log_{10}(L)-9.0377$	kg	mm
Leone et al, 2012	Ozark lake	F	$\log_{10}(W)=3.7286*\log_{10}(L)-9.9905$	kg	mm
Leone et al, 2012	Pool 13	F	$\log_{10}(W)=3.0598*\log_{10}(L)-8.0058$	kg	mm
Leone et al, 2012	Lake Dardanelle	M	$\log_{10}(W)=3.061*\log_{10}(L)-7.98$	kg	mm
Leone et al, 2012	Ozark lake	M	$\log_{10}(W)=2.785*\log_{10}(L)-7.207$	kg	mm
Leone et al, 2012	Pool 13	M	$\log_{10}(W)=2.849*\log_{10}(L)-7.403$	kg	mm
Leone et al, 2013	Pools combined	M	$\log_{10}(W)=2.849*\log_{10}(L)-7.6228$	kg	mm
Tripp et al., 2012	Mississippi		$\log_{10}(W)=3.037*\log_{10}(L)-5.711$	kg	mm
Risely,2012	Mississippi	F	W=2.77e-09*L^3.236	kg	mm
Missouri basin, MICRA	Missouri basin, MICRA	Both	W=4.28e-9*EFL^3.17	kg	mm
Mississippi basin, MICRA	Mississippi basin, MICRA	Both	W=9.66e-10*EFL^3.42	kg	mm
Ohio basin females, MICRA	Ohio basin females, MICRA	F	W=2.08e-8*EFL^2.96	kg	mm
Ohio basin males, MICRA	Ohio basin males, MICRA	M	W=5.29e-9*EFL^3.15	kg	mm
Gulf basin, females MICRA	Gulf basin, females MICRA	F	W=4.86e-9*EFL^3.18	kg	mm
Gulf basin, males MICRA	Gulf basin, males MICRA	M	W=9.66e-10*EFL^3.42	kg	mm

Table 2.7.1. Age of Paddlefish male and female first and full maturity by region.

Area	Source	First maturity males	Full maturity males	First maturity females	Full maturity females
Tennessee and Cumberland Rivers	Timmons and Hughbanks 2000	6	12	8	16
Kentucky Lake	Scholten and Bettoli 2005	4		8	
Kentucky Lake	Hoffnagle and Timmons 1989	6		8	
Lake Francis Case, South Dakota	Pierce et al. 2011	8		11	
Grand Lake	Scarnecchia et al. 2011	6-7	7	8-9	9
Upper Mississippi R	Gengerke 1978	4	9	6	12
Lake Barkley	Bronte and Johnson, 1985	6	8	9-10	
Kentucky Lake	Bronte and Johnson, 1985	7	10		
Oklahoma	Houser and Bross 1959		7		
Montana	Elser, 1976			14	
Lake Cumberland	Hageman et al. 1986	5		8	
Alabama R	Hoxmeier & DeVries 1997			5-6	
Alabama R	Lein & DeVries 1998	5		6	
Arkansas R	Leone et al. 2011			7	14-16
Yellowstone–Sakakawea	Scarnecchia et al. 2007	9	12	15	19
Atchafalaya River and Lake Pontchartrain	Reed 1992		9	6	10
Lower Mississippi R	Risley 2012			10	20
Missouri R	Rosen 1982			8	

Table 2.7.2. Number of gravid, nongravid, total and percent gravid female Paddlefish collected in Lake Dardanelle, Lake Ozark and Pool 13 during pre-spawning season in 2003 -2012.

EFL inches	# Gravid	# Nongravid	# total	% gravid
24	0	1	1	0.00
25	0	0	0	
26	0	2	2	0.00
27	0	0	0	
28	0	1	1	0.00
29	0	0	0	
30	0	1	1	0.00
31	0	1	1	0.00
32	0	27	27	0.00
33	1	22	23	0.04
34	0	23	23	0.00
35	3	37	40	0.08
36	11	37	48	0.23
37	28	36	64	0.44
38	91	51	142	0.64
39	105	33	138	0.76
40	78	31	109	0.72
41	58	23	81	0.72
42	22	11	33	0.67
43	19	5	24	0.79
44	10	4	14	0.71
45	5	0	5	1.00
46	2	1	3	0.67
47	0	0	0	
48	0	0	0	
49	0	1	1	0.00
50	0	0	0	

Table 2.7.3. Number of gravid, nongravid, total and percent gravid female Paddlefish collected in Kentucky Lake, data from Scholten and Bettoli (2005).

EFL inches	# Gravid	# Nongravid	# total	% gravid
32	0	0	0	0.00
33	0	0	0	0.00
34	0	0	0	0.00
35	2	26	28	0.07
36	6	25	31	0.19
37	8	19	27	0.30
38	8	13	21	0.38
39	9	9	18	0.50
40	9	6	15	0.60
41	13	3	16	0.81
42	7	1	8	0.88
43	7	0	7	1.00
44	2	0	2	1.00
45	3	0	3	1.00
46	1	0	1	1.00

Table 2.7.4. Number of gravid, nongravid, total and percent gravid female Paddlefish by size collected in Grand Lake in 2008-20011, data from Oklahoma Department of Wildlife Conservation).

EFL inches	# Gravid	# Nongravid	# total	% gravid
20	0	1	0	0
23	0	1	0	0
25	0	1	0	0
27	0	1	0	0
28	0	5	0	0
29	1	3	1	0.25
30	1	11	1	0.08
31	0	8	0	0.00
32	0	6	0	0.00
33	3	9	3	0.25
34	13	6	13	0.68
35	31	2	31	0.94
36	128	8	128	0.94
37	313	2	313	0.99
38	880	9	880	0.99
39	1942	12	1942	0.99
40	2624	16	2624	0.99
41	2499	7	2499	1.00
42	1822	4	1822	1.00
43	1042	4	1042	1.00
44	590	0	590	1.00
45	256	2	256	0.99
46	118	0	118	1.00
47	28	1	28	0.97
48	17	1	17	0.94
49	4	0	4	1
51	0	1	0	0
52	1	0	1	1
53	1	0	1	1

Table 2.7.5. Number of gravid, nongravid, total and percent gravid female Paddlefish by age collected in Grand Lake in 2008-20011, data from Oklahoma Department of Wildlife Conservation).

Age	# Gravid	# Nongravid	# total	% gravid
4	0	3	3	0
5	0	2	2	0
6	0	1	1	0
7	0	2	2	0
8	18	1	19	0.95
9	1030	15	1045	0.99
10	899	5	904	0.99
11	1453	18	1471	0.99
12	2219	13	2232	0.99
13	326	0	326	1
14	159	0	159	1
15	104	1	105	0.99
16	47	0	47	1
17	22	0	22	1
18	8	0	8	1
19	6	0	6	1
20	2	0	2	1
21	3	0	3	1
23	2	0	2	1
25	1	0	1	1
27	1	0	1	1

Table 2.7.6. Number of gravid, nongravid, total and percent gravid female Paddlefish by size collected in Lower Mississippi River, Arkansas 2008-20011, data from Arkansas Game and Fish Commission (AGFC) Fisheries Division.

EFL inches	# Gravid	# Nongravid	# total	% gravid
16		1	1	0
17		1	1	0
18		1	1	0
21		3	3	0
22		2	2	0
23		1	1	0
24		3	3	0
25		8	8	0
26		13	13	0
27		7	7	0
28		5	5	0
29		5	5	0
30		14	14	0
31		12	12	0
32	2	12	14	0.14
33	3	20	23	0.13
34	6	23	29	0.21
35	7	23	30	0.23
36	10	22	32	0.31
37	8	15	23	0.35
38	10	9	19	0.53
39	3	7	10	0.30
40	8	6	14	0.57
41	1	2	3	0.33
42	1	1	2	0.50
43	1	0	1	1

Table 2.7.7. Number of gravid, nongravid, total and percent gravid female Paddlefish by age collected in Lower Mississippi River, Arkansas 2008-20011, data from Arkansas Game and Fish Commission (AGFC) Fisheries Division.

Age	# Gravid	# Nongravid	# total	% gravid
3		3	3	0
4		3	3	0
5		5	5	0
6		15	15	0
7		21	21	0
8		22	22	0
9		31	31	0
10	8	30	38	0.21
11	11	30	41	0.27
12	10	14	24	0.42
13	7	8	15	0.47
14	5	11	16	0.31
15	3	7	10	0.30
16	4	5	9	0.44
17	5	3	8	0.63
18		7	7	0.00
19	1	1	2	0.50
20	2	0	2	1
21	1	0	1	1
22	1	0	1	1
23	1	0	1	1
24	1	0	1	1

Table 2.7.8. Estimated parameters of maturity schedule described by logistic curve for various stocks.

Stock	Parameter	estimate	st error	Pr(>t)
Arkansas R function of size	M	0.760	0.025	2.00E-16
	k	1.289	0.287	0.00022
	gamma	36.707	0.199	< 2e-16
Kentucky Lake function of size	M	1.045	0.022	2.00E-16
	k	0.575	0.036	9.34E-13
	gamma	39.049	0.142	< 2e-16
Kentucky Lake function of size	M*	1	na	na
	k	0.621	0.034	< 2e-16
	gamma	36.707	0.199	< 2e-16
Grand lake, OK function of size	M	0.932	0.047	<2e-16
	k	2.236	1.430	0.13
	gamma	33.494	0.360	<2e-16
Grand lake, OK function of size	M*	1	na	na
	k	1.9438	1.1371	0.0989
	gamma	33.6001	0.3538	<2e-16
Grand lake, OK function of age	M	0.997	0.001	< 2e-16
	k	13.310	144.400	0.928
	gamma	0.779	2.402	0.005
Lower Mississippi R function of size	M	0.45905	0.05035	9.63E-07
	k	0.61309	0.22756	0.0195
	gamma	34.55391	0.74723	6.83E-15
Lower Mississippi R 2 inch size intervals	M*	0.72512	0.0799	1.00E-04
	k	0.3756	0.06661	0.00133
	gamma	37.63001	0.82447	7.41E-09
Lower Mississippi R function of size	M*	1	na	na
	k	0.30657	0.07404	0.00051
	gamma	16.41321	0.84027	1.69E-14

Table 2.7.9. Summary of estimated maturity schedule as a function of size and age for various stocks.

age	Arkansas R Lake Dardanelle	Arkansas R Lake Ozark	Arkansas R Pool 13	Arkansas R Pools combined	Kentucky Lake	Arkansas R Grand Lake	Lower Mississippi R
1	0.00	0.00	0.00	0.00	0.00	0.00	0.01
2	0.00	0.00	0.00	0.00	0.00	0.00	0.01
3	0.00	0.00	0.00	0.00	0.00	0.00	0.02
4	0.00	0.00	0.00	0.00	0.00	0.00	0.02
5	0.00	0.00	0.00	0.00	0.00	0.12	0.03
6	0.00	0.00	0.00	0.00	0.01	0.87	0.04
7	0.00	0.00	0.00	0.00	0.04	0.93	0.05
8	0.03	0.01	0.00	0.00	0.12	0.93	0.07
9	0.17	0.06	0.02	0.03	0.28	0.93	0.09
10	0.47	0.20	0.10	0.16	0.48	0.93	0.12
11	0.66	0.42	0.29	0.45	0.66	0.93	0.16
12	0.72	0.59	0.50	0.66	0.79	0.93	0.21
13	0.75	0.67	0.64	0.73	0.86	0.93	0.26
14	0.75	0.71	0.70	0.75	0.91	0.93	0.32
15	0.76	0.73	0.73	0.76	0.93	0.93	0.39
16	0.76	0.74	0.74	0.76	0.95	0.93	0.47
17	0.76	0.75	0.75	0.76	0.96	0.93	0.54
18	0.76	0.75	0.75	0.76	0.97	0.93	0.62
19	0.76	0.75	0.75	0.76	0.97	0.93	0.69
20	0.76	0.75	0.76	0.76	0.98	0.93	0.75
21	0.76	0.75	0.76	0.76	0.98	0.93	0.80
22	0.76	0.76	0.76	0.76	0.98	0.93	0.85
23	0.76	0.76	0.76	0.76	0.98	0.93	0.88
24	0.76	0.76	0.76	0.76	0.98	0.93	0.91
25	0.76	0.76	0.76	0.76	0.99	0.93	0.93
26	0.76	0.76	0.76	0.76	0.99	0.93	0.95
27	0.76	0.76	0.76	0.76	0.99	0.93	0.96
28	0.76	0.76	0.76	0.76	0.99	0.93	0.97
29	0.76	0.76	0.76	0.76	0.99	0.93	0.98
30	0.76	0.76	0.76	0.76	0.99	0.93	0.98

Table 2.8.1. Fecundity as a function length and weight reported for selected stocks of Paddlefish.

citation	Water body	egg diameter	ovary weight	egg/kg body weight
Genderke 1978	Upper Mississippi			16,900
Rosen et al. 1982	Missour River	2.0 - 2.5 mm		
Russell and others cited in Reed et al.1992	Osage River			26,000
Scholten and Bettoli 2005	Kentucky Lake	1.3 to 3.2 mm	0.957 to 4.884 kg	range 9,281 to 26,374
		mean 2.33 mm; SE 0.01 mm	mean= 2.310 kg; SE = 0.093	(mean 16,381; SE 5 417
Hageman et al. 1986	Cumberlaand Lake	mean of 2.0 mm in October to 3.0 mm in April		
Leone et al, 2011	Arkansas River		1,255–3,865 g	7,794 to 30,247
			mean 2,291 ± 53 g	mean 15,945 ± 404.
Risely 2012	Lower Mississippi		961 to 3,943 g	12,321 to 25,753
	River		mean 2,124 g, SE = 86.3	mean = 18,777, SE = 371
Reed et al. 1992	Lake Pontchartrain	2.1 to 3.1 mm	na	6,600 to 13,300
		mean 2.67 mm (SE= 0.2)		mean = 9,484; SE= 696
Lein and DeVries,1998	Alabama River	2.20 to 2.85 mm	na	19,414 +- 3,420
		2.62 +- 0.03		14,889 to 22,975
Rider et al 2011	Alabama River	2.2 to 3.4	0.74 to 3.59 kg	7,550 to 21,116
		mean 2.75 mm, SE = 0.01	mean = 1.98 kg; SE = 0.229	mean = 15,794, SE = 1,326

Table 2.8.2. Fecundity as a function length and weight reported for selected stocks of Paddlefish.

Data source	Water body	System	Fecundity function
Genderke 1978	Upper Mississippi R	Upper Mississippi R	#ova = 920.9 *FL - 942,900
Genderke 1978	Upper Mississippi R	Upper Mississippi R	#ova = 27,779*weight - 192,800
Scholten and Bettoli 2005	Kentucky Lake	Tennessee River	$log10(\#ova) = 3.236*log10(EFL) - 4.284 (r^2=0.48)$
Scholten and Bettoli 2005	Kentucky Lake	Tennessee River	$log10(\#ova)) = 4.282 + 0.937*log10(weight) r^2=0.38)$
Leone et al. 2012	Lake Dardanelle	Arkansas River	log10(#ova)= 4.9357 + 0.4279*log10 (weight)
Leone et al. 2012	Lake Dardanelle	Arkansas River	log10(#ova)=1.6518 +1.2708*log10 (EFL)
Leone et al. 2012	Ozark lake	Arkansas River	log10(#ova)= 4.316 + 08657*log10 (weight)
Leone et al. 2012	Ozark lake	Arkansas River	log10(#ova)=-5.6298 +3.6654*log10 (EFL)
Leone et al. 2012	all combined	Arkansas River	$log10(\#ova) = 4.348 + 0.863 *log10 (weight) (r^2=0.19)$
Leone et al. 2012	all combined	Arkansas River	$log10(\#ova) = 2.011*log10 (EFL) - 0.650(r^2=0.09)$
Leone et al. 2012	Pool 13	Arkansas River	log10(#ova) =4.6967 + 0.5514*log10 (weight)
Leone et al. 2013	Pool 13	Arkansas River	log10(#ova)=4.8798 + 0.1493*log10 (EFL)
Risely 2012	Lower Mississippi R	Mississippi R	#ova= 20,627 *weight – 22,860
Risely 2012	Lower Mississippi R	Mississippi R	#ova = 751.67*(EFL) – 472,367
Reed et al. 1992	Lake Pontchartrain	Lake Pontchartrain	log10(#ova) = 4.29 + 0.68l*og10 (weight)
Lein and DeVries 1998	Tallapoosa and	Alabama River	$\#ova=31,656.6 (weight) - 205121(r^2=0.93)$
Lein and DeVries 1998	Cahaba rivers	Alabama River	$\#ova= 1,614.2* (EFL) - 1,290,063(r^2=0.89)$
Rider et al. 2011	Alabama River	Alabama River	log10(#ova) = 3.294 + 0.869 Log10 (weight);
Rider et al. 2011	Alabama River	Alabama River	log10(#ova) =4.819*Log10 (EFL) -9.078

Table 2.9.1. Input variables for natural mortality rate calculation.

Citation	Water body	Sex	t0	K	Linf	max age reported	Tmax assumed	age of maturity	length of maturity
Scarnecchia et al. 2008	Sakakawea Lake	F	-2.1451	0.10	124.6	55	60	15	103.00
Scarnecchia et al. 2008	Yellowstone R	F	-3.2195	0.11	118.4	55	60	15	103.00
Rosen et al. 1982	Missour River	F	-2.215	0.17	90.3	26	50	8	75.00
Pierce et al. 2011	Lake Francis	Both	-1.68	0.10	132.5	43	50	11	103.00
Pierce et al. 2011	Lake Francis	F	1.19	0.16	130.1	43	50	11	103.00
Tripp et all. 2012	Mississippi		-4.334	0.10	113.4	20	20	9	83.50
Bronte & Johnson 1985	Lake Barkley	F	-0.217	0.15	116.3	12	15	9	87.90
Bronte & Johnson 1985	Kentucky Lake	F	-0.534	0.13	112.4	14	15	9	81.00
Hoffnagle & Timmons 1989	Kentucky Lake	Both	-0.67583	0.11	113.0	16	25	8	70.53
Scholten and Bettoli 2005	Kentucky Lake	Both	-1.53	0.13	127.9	11	25	8	90.80
Scholten and Bettoli 2005	Kentucky Lake	F	-0.91	0.14	130.0	11	25	8	92.00
Scholten re-estimated	Kentucky Lake	Both	-0.77	0.23	103.5	11	25	8	89.50
Scholten re-estimated	Kentucky Lake	F	-0.32	0.18	120.2	11	25	8	92.40
Combs 1982	Grand Lake and Neosho River	Both	-2.85203	0.10	146.9	13	30	8	96.00
Paukert and Fisher 2001	Keystone Reservoir	Both	-0.12646	0.43	105.8	14	30	8	96.00
Scarnecchia et al. 2011	Grand Lake	F	NA	0.23	112.3	27	30	8	96.00
Scarnecchia et al. 2011	Grand Lake	F	-10.774	0.07	133.6	27	30	8	96.00
This study	Grand Lake	F	-4.1346	0.23	105.9	27	30	8	96.00
This study	Grand Lake+ MICRA data	F	-1.82	0.20	110.9	27	30	8	96.00
Leone et al. 2011	Dardanelle lake	F	-0.328	0.19	110.5	16	20	7	86.83

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Study	Location	Sex							
Leone et al. 2011	Ozark Lake	F	-0.329	0.20	104.5	16	20	7	84.75
Leone et al. 2011	Pool 13	F	-0.359	0.18	106.5	16	20	7	82.25
Leone et al. 2011	All combined	F	-1.115	0.13	117.8	16	20	7	82.43
Tripp et all. 2012	Mississippi		-2.649	0.13	113.2	20	20	9	88.30
Tripp et all. 2012	Mississippi		-4.383	0.09	118.5	20	20	9	84.80
Risely 2012	Mississippi	both	-0.995	0.14	108.2	24	30	10	83.80
Risely 2012	Mississippi	F	-0.940	0.14	108.3	24	30	10	84.90
Reed et al. 1992	Lake Pontchartrain	Both	-0.71	0.28	120.5	14	15	8	109.61
Reed et al. 1992	Lake Henderson	Both	-0.731	0.30	102.8	9	15	8	95.50
Reed et al. 1992	Atchafalaya River	Both	-1.019	0.25	110.2	9	15	8	99.05
Hoxmeier and Devries 1997	lower Alabama River	Both	-0.0667	0.12	127.6	11	20	6	79.70
Lein and Devries 1998	Tallapoosa River	F	-0.2761	0.18	110.5	9	20	6	79.70
Lein and Devries 1998	Claiborne lock	Both	-0.0895	0.23	106.7	11	20	6	79.70
Lein and Devries 1998	Cahaba River	Both	-0.1545	0.21	102.8	11	20	6	79.70
Rider et al. 2011	Alabama River	Both	-1.364	0.16	103.7	17	17	7	79.70
This study	Gulf Basin	both	-1.06859	0.49	97.7	17	20	8	96.60
This study	Mississippi Basin	both	-0.58258	0.60	99.0		30	9	98.70
This study	Missouri Basin	both	-2.03046	0.23	94.5	55	55	11	90.00
This study	Ohio Basin	both	-0.70139	0.42	101.5		30	8	99.00

Table 2.9.1. Input variables for natural mortality rate calculation.

Citation	Water body	Sex	t0	K	L∞	max age reported	Tmax	age of maturity	length of maturity	mean annual temp, C
Scarnecchia et al 2008 mgmt plan	Sakakawea Lake	F	-2.1451	0.10	124.6	55	60	15	103.00	9.60
Scarnecchia et al 2008 mgmt plan	Yellowstone R	F	-3.2195	0.11	118.4	55	60	15	103.00	9.60
Rosen et al. 1982	Missour River	F	-2.215	0.17	90.3	26	50	8	75.00	11.20
Pierce et al, 2011	Lake Francis	Both	-1.68	0.10	132.5	43	50	11	103.00	11.20
Pierce et al, 2011	Lake Francis	F	1.19	0.16	130.1	43	50	11	103.00	11.20
Tripp et all, 2012	Mississippi		-4.334	0.10	113.4	20	20	9	83.50	14.80
Bronte & Johnson 1985	Lake Barkley	F	-0.217	0.15	116.3	12	15	9	87.90	17.70
Bronte & Johnson 1985	Kentucky Lake	F	-0.534	0.13	112.4	14	15	9	81.00	17.70
Hoffnagle & Timmons 1989	Kentucky Lake	Both	-0.67583	0.11	113.0	16	25	8	70.53	17.70
Scholten & Bettoli 2005	Kentucky Lake	Both	-1.53	0.13	127.9	11	25	8	90.80	17.70
Scholten & Bettoli 2005	Kentucky Lake	F	-0.91	0.14	130.0	11	25	8	92.00	17.70
Scholten reestimated	Kentucky Lake	Both	-0.77	0.23	103.5	11	25	8	89.50	17.70
Scholten reestimated	Kentucky Lake	F	-0.32	0.18	120.2	11	25	8	92.40	17.70
Combs 1982	Grand Lake and Neosho River	Both	-2.85203	0.10	146.9	13	30	8	96.00	18.70
Paukert and Fisher 2001	Keystone Reservoir	Both	-0.12646	0.43	105.8	14	30	8	96.00	18.70
Scarnecchia et al. 2011	Grand Lake	F	NA	0.23	112.3	27	30	8	96.00	18.70
Scarnecchia et al. 2011	Grand Lake	F	-10.774	0.07	133.6	27	30	8	96.00	18.70
This study	Grand Lake	F	-4.1346	0.23	105.9	27	30	8	96.00	18.70
This study	Grand Lake+ MICRA	F	-1.82	0.20	110.9	27	30	8	96.00	18.70
Leone et al. 2011	Dardanelle lake	F	-0.328	0.19	110.5	16	20	7	86.83	18.70
Leone et al. 2011	Ozark Lake	F	-0.329	0.20	104.5	16	20	7	84.75	18.86
Leone et al. 2011	Pool 13	F	-0.359	0.18	106.5	16	20	7	82.25	18.64

Study	Location	Sex								
Leone et al. 2011	All combined	F	-1.115	0.13	117.8	16	20	7	82.43	18.66
Tripp et all, 2012	Mississippi		-2.649	0.13	113.2	20	20	9	88.30	17.10
Tripp et all, 2012	Mississippi		-4.383	0.09	118.5	20	20	9	84.80	17.10
Risely, 2012	Mississippi	both	-0.995	0.14	108.2	24	30	10	83.80	17.10
Risely, 2012	Mississippi	F	-0.940	0.14	108.3	24	30	10	84.90	17.10
Reed et al. 1992	Lake Pontchartrain	Both	-0.71	0.28	120.5	14	15	8	109.61	22.00
Reed et al. 1992	Lake Henderson	Both	-0.731	0.30	102.8	9	15	8	95.50	22.00
Reed et al. 1992	Atchafalaya River	Both	-1.019	0.25	110.2	9	15	8	99.05	22.00
Hoxmeier & Devries 1997	lower Alabama River	Both	-0.0667	0.12	127.6	11	20	6	79.70	22.00
Lein & Devries 1998	Tallapoosa River	F	-0.2761	0.18	110.5	9	20	6	79.70	22.00
Lein & Devries 1998	Claiborne lock	Both	-0.0895	0.23	106.7	11	20	6	79.70	22.00
Lein & Devries 1998	Cahaba River	Both	-0.1545	0.21	102.8	11	20	6	79.70	22.00
Rider et al. 2011	Alabama River	Both	-1.364	0.16	103.7	17	17	7	79.70	22.00
This study	Gulf Basin	both	-1.06859	0.49	97.7	17	20	8	96.60	22.00
This study	Mississippi Basin	both	-0.58258	0.60	99.0		30	9	98.70	17.00
This study	Missouri Basin	both	-2.03046	0.23	94.5	55	55	11	90.00	10.40
This study	Ohio Basin	both	-0.70139	0.42	101.5		30	8	99.00	

Table 2.9.2. Input variables for natural mortality rate calculation.

Citation	Water body	Sex	Empirical estimate	rule of thumb	Hewit and Hoenig	Hoenig geometric mean regression	Secharan, 1975	Alverson and Carney
Scarnecchia et al. 2008	Sakakawea Lake	F		0.05	0.07	0.05	0.08	0.03
Scarnecchia et al. 2008	Yellowstone R	F		0.05	0.07	0.05	0.08	0.03
Rosen et al. 1982	Missouri River	F		0.06	0.08	0.06	0.09	0.02
Pierce et al. 2011	Lake Francis	Both		0.06	0.08	0.06	0.09	0.05
Pierce et al. 2011	Lake Francis	F		0.06	0.08	0.06	0.09	0.02
Tripp et al. 2012	Mississippi			0.15	0.21	0.18	0.23	0.26
Bronte and Johnson 1985	Lake Barkley	F		0.2	0.28	0.26	0.31	0.33
Bronte and Johnson 1985	Kentucky Lake	F	0.08	0.2	0.28	0.26	0.31	0.35
Hoffnagle and Timmons 1989	Kentucky Lake	Both		0.12	0.17	0.14	0.18	0.18
Scholten and Bettoli 2005	Kentucky Lake	Both		0.12	0.17	0.14	0.18	0.16
Scholten and Bettoli 2005	Kentucky Lake	F		0.12	0.17	0.14	0.18	0.15
Scholten re-estimated	Kentucky Lake	Both		0.12	0.17	0.14	0.18	0.09
Scholten re-estimated	Kentucky Lake	F		0.12	0.17	0.14	0.18	0.12
Combs 1982	Grand Lake and Neosho River	Both		0.1	0.14	0.11	0.15	0.14
Paukert and Fisher 2001	Keystone Reservoir	Both		0.1	0.14	0.11	0.15	0.01
Scarnecchia et al. 2011	Grand Lake	F		0.1	0.14	0.11	0.15	0.05
Scarnecchia et al. 2011	Grand Lake	F		0.1	0.14	0.11	0.15	0.17
This study	Grand Lake	F		0.1	0.14	0.11	0.15	0.05
This study	Grand Lake+ MOCRA data	F		0.1	0.14	0.11	0.15	0.07
Leone et al. 2011	Dardanelle lake	F	0.07	0.15	0.21	0.18	0.23	0.18
Leone et al. 2011	Ozark Lake	F	0.07	0.15	0.21	0.18	0.23	0.17
Leone et al. 2011	Pool 13	F	0.07	0.15	0.21	0.18	0.23	0.19

Leone et al. 2011	All combined	F	0.07	0.15	0.21	0.18	0.23	0.23
Tripp et al. 2012	Mississippi			0.15	0.21	0.18	0.23	0.23
Tripp et al. 2012	Mississippi			0.15	0.21	0.18	0.23	0.27
Risely 2012	Mississippi	both		0.1	0.14	0.11	0.15	0.11
Risely 2012	Mississippi	F		0.1	0.14	0.11	0.15	0.11
Reed et al. 1992	Lake Pontchartrain	Both	0.35	0.2	0.28	0.26	0.31	0.22
Reed et al. 1992	Lake Henderson	Both	0.35	0.2	0.28	0.26	0.31	0.20
Reed et al. 1992	Atchafalaya River	Both	0.35	0.2	0.28	0.26	0.31	0.23
Hoxmeier and Devries 1997	lower Alabama River	Both	0.35	0.15	0.21	0.18	0.23	0.24
Lein and Devries 1998	Tallapoosa River	F	0.35	0.15	0.21	0.18	0.23	0.18
Lein and Devries 1998	Claiborne lock	Both	0.35	0.15	0.21	0.18	0.23	0.15
Lein and Devries 1998	Cahaba River	Both	0.35	0.15	0.21	0.18	0.23	0.16
Rider et al. 2011	Alabama River	Both	0.35	0.18	0.25	0.22	0.27	0.27
This study	Gulf Basin	both		0.15	0.21	0.18	0.23	0.04
This study	Mississippi Basin	both		0.10	0.14	0.11	0.15	0.00
This study	Missouri Basin	both		0.05	0.08	0.05	0.08	0.01
This study	Ohio Basin	both		0.10	0.14	0.11	0.15	0.01

Table 2.9.2. continues.

Citation	Water body	Sex	Roff 1984	Rikhter and Efanov's	Charnov and Berrigan	Ralston 1987	Ralston method 2	Jensen first
Scarnecchia et al. 2008	Sakakawea Lake	F	0.08	0.06	0.15	0.19	0.15	0.11
Scarnecchia et al. 2008	Yellowstone R	F	0.07	0.06	0.15	0.22	0.19	0.11
Rosen et al. 1982	Missour River	F	0.17	0.19	0.28	0.37	0.37	0.21
Pierce et al. 2011	Lake Francis	Both	0.15	0.12	0.20	0.19	0.14	0.15
Pierce et al. 2011	Lake Francis	F	0.10	0.12	0.20	0.34	0.33	0.15
Tripp et al. 2012	Mississippi		0.21	0.16	0.24	0.19	0.14	0.18
Bronte and Johnson 1985	Lake Barkley	F	0.15	0.16	0.24	0.32	0.31	0.18
Bronte and Johnson 1985	Kentucky Lake	F	0.17	0.16	0.24	0.27	0.25	0.18
Hoffnagle and Timmons 1989	Kentucky Lake	Both	0.23	0.19	0.28	0.22	0.18	0.21
Scholten and Bettoli 2005	Kentucky Lake	Both	0.21	0.19	0.28	0.26	0.23	0.21
Scholten and Bettoli 2005	Kentucky Lake	F	0.21	0.19	0.28	0.28	0.26	0.21
Scholten re-estimated	Kentucky Lake	Both	0.13	0.19	0.28	0.51	0.54	0.21
Scholten re-estimated	Kentucky Lake	F	0.17	0.19	0.28	0.38	0.38	0.21
Combs 1982	Grand Lake and Neosho River	Both	0.25	0.19	0.28	0.18	0.14	0.21
Paukert and Fisher 2001	Keystone Reservoir	Both	0.04	0.19	0.28	1.02	1.19	0.21
Scarnecchia et al. 2011	Grand Lake	F	0.13	0.19	0.28	0.51	0.55	0.21
Scarnecchia et al. 2011	Grand Lake	F	0.28	0.19	0.28	0.10	0.04	0.21
This study	Grand Lake	F	0.13	0.19	0.28	0.51	0.55	0.21
This study	Grand Lake+ MOCRA data	F	0.15	0.19	0.28	0.44	0.46	0.21
Leone et al. 2011	Dardanelle lake	F	0.21	0.22	0.31	0.40	0.41	0.24
Leone et al. 2011	Ozark Lake	F	0.20	0.22	0.31	0.44	0.46	0.24
Leone et al. 2011	Pool 13	F	0.22	0.22	0.31	0.38	0.38	0.24

Leone et al. 2011	All combined	F	0.26	0.22	0.31	0.27	0.24	0.24
Tripp et al. 2012	Mississippi		0.18	0.16	0.24	0.26	0.23	0.18
Tripp et all, 2012	Mississippi		0.21	0.16	0.24	0.17	0.12	0.18
Risely 2012	Mississippi	both	0.14	0.13	0.22	0.27	0.25	0.17
Risely 2012	Mississippi	F	0.14	0.13	0.22	0.29	0.27	0.17
Reed et al. 1992	Lake Pontchartrain	Both	0.10	0.19	0.28	0.63	0.70	0.21
Reed et al. 1992	Lake Henderson	Both	0.09	0.19	0.28	0.70	0.78	0.21
Reed et al. 1992	Atchafalaya River	Both	0.11	0.19	0.28	0.57	0.63	0.21
Hoxmeier and Devries 1997	lower Alabama River	Both	0.34	0.26	0.37	0.23	0.19	0.28
Lein and Devries 1998	Tallapoosa River	F	0.28	0.26	0.37	0.39	0.40	0.28
Lein and Devries 1998	Claiborne lock	Both	0.23	0.26	0.37	0.51	0.55	0.28
Lein and Devries 1998	Cahaba River	Both	0.25	0.26	0.37	0.47	0.49	0.28
Rider et al. 2011	Alabama River	Both	0.23	0.22	0.31	0.33	0.32	0.24
This study	Gulf Basin	both	0.03	0.19	0.28	1.16	1.36	0.21
This study	Mississippi Basin	both	0.01	0.16	0.24	1.45	1.73	0.18
This study	Missouri Basin	both	0.06	0.12	0.20	0.53	0.57	0.15
This study	Ohio Basin	both	0.04	0.19	0.28	1.00	1.16	0.21

Table 2.9.2. continues

Source	Water body	Sex	Jensen second	Frisk	Pauly	Roffs second estimator	Gunderson
Scarnecchia et al 2008	Sakakawea Lake	F	0.15	0.17	0.16	0.06	0.36
Scarnecchia et al 2008	Yellowstone R	F	0.17	0.18	0.18	0.05	0.36
Rosen et al. 1982	Missour River	F	0.26	0.21	0.27	0.11	0.36
Pierce et al. 2011	Lake Francis	Both	0.15	0.17	0.17	0.09	0.36
Pierce et al. 2011	Lake Francis	F	0.24	0.20	0.24	0.13	0.36
Tripp et al. 2012	Mississippi		0.15	0.17	0.18	0.11	0.36
Bronte and Johnson 1985	Lake Barkley	F	0.23	0.20	0.26	0.15	0.36
Bronte and Johnson 1985	Kentucky Lake	F	0.20	0.19	0.24	0.16	0.36
Hoffnagle and Timmons 1989	Kentucky Lake	Both	0.17	0.17	0.21	0.20	0.36
Scholten and Bettoli 2005	Kentucky Lake	Both	0.20	0.19	0.23	0.16	0.36
Scholten and Bettoli 2005	Kentucky Lake	F	0.21	0.19	0.24	0.17	0.36
Scholten re-estimated	Kentucky Lake	Both	0.34	0.23	0.36	0.11	0.36
Scholten re-estimated	Kentucky Lake	F	0.26	0.21	0.29	0.16	0.36
Combs 1982	Grand Lake and Neosho River	Both	0.15	0.17	0.18	0.16	0.36
Paukert and Fisher 2001	Keystone Reservoir	Both	0.65	0.31	0.58	0.13	0.36
Scarnecchia et al. 2011	Grand Lake	F	0.34	0.24	0.36	0.12	0.36
Scarnecchia et al. 2011	Grand Lake	F	0.10	0.14	0.14	0.08	0.36
This study	Grand Lake	F	0.35	0.24	0.37	0.07	0.36
This study	Grand Lake+ MOCRA data	F	0.30	0.22	0.33	0.09	0.36
Leone et al. 2011	Dardanelle lake	F	0.28	0.21	0.31	0.15	0.36
Leone et al. 2011	Ozark Lake	F	0.30	0.22	0.33	0.14	0.36
Leone et al. 2011	Pool 13	F	0.27	0.21	0.30	0.16	0.36
Leone et al. 2011	All combined	F	0.20	0.19	0.24	0.17	0.36

Tripp et al. 2012	Mississippi		0.20	0.19	0.23	0.11	0.36
Tripp et al. 2012	Mississippi		0.14	0.16	0.18	0.11	0.36
Risely 2012	Mississippi	both	0.20	0.19	0.24	0.12	0.36
Risely 2012	Mississippi	F	0.21	0.19	0.25	0.12	0.36
Reed et al. 1992	Lake Pontchartrain	Both	0.41	0.25	0.42	0.08	0.36
Reed et al. 1992	Lake Henderson	Both	0.45	0.26	0.47	0.07	0.36
Reed et al. 1992	Atchafalaya River	Both	0.38	0.25	0.41	0.09	0.36
Hoxmeier and Devries 1997	lower Alabama River	Both	0.18	0.18	0.22	0.21	0.36
Lein and Devries 1998	Tallapoosa River	F	0.27	0.21	0.31	0.21	0.36
Lein and Devries 1998	Claiborne lock	Both	0.34	0.23	0.38	0.23	0.36
Lein and Devries 1998	Cahaba River	Both	0.32	0.23	0.36	0.18	0.36
Rider et al. 2011	Alabama River	Both	0.24	0.20	0.29	0.14	0.36
This study	Gulf Basin	both	0.73	0.32	0.67	0.02	0.36
This study	Mississippi Basin	both	0.90	0.35	0.74	0.00	0.36
This study	Missouri Basin	both	0.35	0.24	0.33	0.03	0.36
This study	Ohio Basin	both	0.63	0.30	0.00	0.03	0.36

Table 2.10.1. Estimates and confidence intervals for parameters from the yearclass curve model for the reach Lake Francis Case, South Dakota.

Variable	Estimate	Lower 95% CI	Upper 95% CI
Z	0.177	0.143	0.219
N_95	27.0	13.9	52.5
N_94	23.0	12.0	44.3
N_93	36.1	19.0	68.6
N_92	6.5	3.3	12.5
N_91	40.6	21.5	76.6
s_3	0.158	0.052	0.482
s_4	0.532	0.198	1.434
s_5	1.092	0.456	2.616
s_6	1.133	0.478	2.684
s_7	0.978	0.416	2.299
s_8	0.955	0.409	2.233
s_9	0.851	0.365	1.985
s_10	0.745	0.320	1.735
q_95	0.937	0.618	1.420
q_96	0.94	0.62	1.41
q_97	1.00	0.67	1.49
q_98	1.10	0.74	1.63
q_99	1.08	0.73	1.60
q_00	0.96	0.65	1.42
q_01	0.94	0.64	1.39
q_02	0.91	0.62	1.35
q_03	0.82	0.55	1.21
q_04	0.89	0.61	1.32
q_05	1.06	0.72	1.57
q_06	1.03	0.69	1.52
q_07	1.03	0.70	1.52
q_08	1.30	0.87	1.93
q_09	1.23	0.83	1.83
q_10	1.14	0.77	1.70
q_11	0.69	0.46	1.03

Table 2.10.2. Estimated total instantaneous mortality rates (Z, per year) from year-specific catch curve analyses.

Collection	State	Year	Ages	Z	Lower 95% CI	Upper 95% CI
Quinn	AR	2003-2004	9-12	1.350	2.382	0.319
Tripp et al.	AR	2011	12-20	0.495	0.678	0.312
Tripp et al.	MO	2011	13-19	0.499	1.037	-0.038

Table 2.10.3. Estimated total instantaneous mortality rates (Z) and their standard errors (SE) for Paddlefish in a range of systems in Tennessee (TN) and Mississippi (MS). Years refers to the years included in the analysis, with 2008 indicating the 2008-2009 season and 2012 indicating the 2011-2012 season.

System	Years	Z	SE	Min. size
Barclay Reservoir (TN)	2008-2012	0.53	0.028	36
Cheatham Reservoir (TN)	2008-2012	0.59	0.037	36
Mississippi (TN)	2008-2012	0.89	0.023	34
Kentucky Lake (TN)	2008-2012	0.30	0.005	36
Cumberland Reservoir (TN)	2010-2012	0.88	0.092	36
Sunflower River (MS)	2010-2012	1.02	0.041	37
Mississippi (MS)	2008-2012	0.67	0.031	34
Moon Lake (MS)	2010-2011	NA		37
4 Mile Lake (MS)	2010-2012	0.64	0.105	37
Delta Zone (MS)	2010-2012	0.54	0.011	37

Table 3.1.1. Partial recruitment vectors (selectivity) for Kentucky Lake Paddlefish under various minimum legal sizes (inches).

age	minimum size, inches													
	24	25	26	27	28	29	30	31	32	33	34	35	36	37
1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
4	0.83	0.56	0.26	0.08	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
5	1.00	1.00	0.97	0.89	0.71	0.44	0.20	0.06	0.01	0.00	0.00	0.00	0.00	0.00
6	1.00	1.00	1.00	1.00	0.99	0.96	0.87	0.69	0.44	0.22	0.08	0.02	0.00	0.00
7	1.00	1.00	1.00	1.00	1.00	1.00	0.99	0.97	0.91	0.77	0.57	0.34	0.16	0.06
8	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	0.97	0.91	0.78	0.58	0.37
9	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	0.95	0.87	0.73
10	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	0.97	0.91
11	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	0.97
12	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99
13	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
14	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
15	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
16	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
17	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
18	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
19	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
20	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
21	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
22	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
23	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
24	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
25	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
26	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
27	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
28	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
29	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
30	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

Table 3.1.2. Reference points from yield per recruit analysis for Lake Sakakawea, North Dakota (M = 0.07).

Ref Point	Minimum size, inches						
	32	33	34	35	36	37	38
Fmax	0.26	0.29	0.34	0.4	0.48	0.62	0.83
F0.1	0.09	0.09	0.09	0.1	0.1	0.1	0.11
YPR_{max}	6.63	6.74	6.84	6.93	7.01	7.09	7.14
F40% MSP	0.05	0.05	0.05	0.05	0.05	0.06	0.06
F30% MSP	0.06	0.06	0.07	0.07	0.07	0.08	0.08
M	0.07	0.07	0.07	0.07	0.07	0.07	0.07
Tmax	60	60	60	60	60	60	60
Z at F40%	0.12	0.12	0.12	0.12	0.12	0.13	0.13
Z at F30%	0.13	0.13	0.14	0.14	0.14	0.15	0.15
U at F40%	0.04	0.04	0.05	0.05	0.05	0.05	0.06
U at F30%	0.06	0.06	0.06	0.07	0.07	0.07	0.08

Table 3.1.3. Reference points from yield per recruit analysis for Lake Francis Case, South Dakota (M = 0.07).

Ref Point	Minimum size, inches						
	32	33	34	35	36	37	38
Fmax	0.18	0.2	0.21	0.23	0.25	0.28	0.31
F0.1	0.08	0.09	0.09	0.09	0.09	0.1	0.1
YPR_{max}	5.34	5.45	5.54	5.65	5.75	5.85	5.94
F40% MSP	0.06	0.06	0.06	0.06	0.06	0.07	0.07
F30% MSP	0.08	0.08	0.08	0.09	0.09	0.09	0.1
M	0.07	0.07	0.07	0.07	0.07	0.07	0.07
Tmax	50	50	50	50	50	50	50
Z at F40%	0.13	0.13	0.13	0.13	0.13	0.14	0.14
Z at F30%	0.15	0.15	0.15	0.16	0.16	0.16	0.17
U at F40%	0.05	0.06	0.06	0.06	0.06	0.06	0.06
U at F30%	0.07	0.08	0.08	0.08	0.08	0.09	0.09

Table 3.1.4. Reference points from yield per recruit analysis for Kentucky Lake, TN (M = 0.08).

Ref Point	Minimum size, inches						
	32	33	34	35	36	37	38
F0.1	0.11	0.11	0.11	0.12	0.12	0.13	0.13
Fmax	0.2	0.22	0.24	0.26	0.29	0.33	0.38
YPRmax	7.81	7.98	8.14	8.31	8.47	8.62	8.77
F40% MSP	0.08	0.08	0.08	0.09	0.09	0.1	0.11
F30% MSP	0.1	0.11	0.11	0.12	0.13	0.14	0.15
M	0.08	0.08	0.08	0.08	0.08	0.08	0.08
Tmax	30	30	30	30	30	30	30
Z at F40%	0.16	0.16	0.16	0.17	0.17	0.18	0.19
Z at F30%	0.18	0.19	0.19	0.2	0.21	0.22	0.23
U at F40%	0.07	0.07	0.08	0.08	0.08	0.09	0.1
U at F30%	0.1	0.1	0.1	0.11	0.12	0.12	0.13

Table 3.1.5. Reference points from yield per recruit analysis for Kentucky Lake, TN (M = 0.14).

Ref Point	Minimum size, inches						
	32	33	34	35	36	37	38
F0.1	0.16	0.16	0.17	0.18	0.18	0.19	0.2
Fmax	0.44	0.51	0.6	0.72	0.91	N/A	N/A
YPRmax	4.55	4.63	4.71	4.78	4.84	N/A	N/A
F40% MSP	0.09	0.1	0.1	0.11	0.11	0.12	0.14
F30% MSP	0.12	0.13	0.14	0.15	0.16	0.17	0.2
M	0.14	0.14	0.14	0.14	0.14	0.14	0.14
Tmax	30	30	30	30	30	30	30
Z at F40%	0.23	0.24	0.24	0.25	0.25	0.26	0.28
Z at F30%	0.26	0.27	0.28	0.29	0.3	0.31	0.34
U at F40%	0.08	0.08	0.09	0.09	0.1	0.11	0.12
U at F30%	0.11	0.11	0.12	0.13	0.14	0.15	0.17

Table 3.1.6. Reference points from yield per recruit analysis for Kentucky Lake, TN (M = 0.20).

Ref Point	Minimum size, inches						
	32	33	34	35	36	37	38
F0.1	0.24	0.25	0.26	0.28	0.29	0.31	0.33
Fmax	N/A	N/A	N/A	N/A	N/A	N/A	N/A
YPRmax	N/A	N/A	N/A	N/A	N/A	N/A	N/A
F40% MSP	0.12	0.13	0.14	0.15	0.16	0.19	0.21
F30% MSP	0.16	0.17	0.19	0.2	0.23	0.26	0.3
M	0.2	0.2	0.2	0.2	0.2	0.2	0.2
Tmax	21	21	21	21	21	21	21
Z at F40%	0.32	0.33	0.34	0.35	0.36	0.39	0.41
Z at F30%	0.36	0.37	0.39	0.4	0.43	0.46	0.5
U at F40%	0.1	0.11	0.12	0.13	0.14	0.15	0.18
U at F30%	0.14	0.15	0.16	0.17	0.18	0.21	0.24

Table 3.1.7. Reference points from yield per recruit analysis for Arkansas River, Arkansas (M = 0.07).

Ref Point	Minimum size, inches						
	32	33	34	35	36	37	38
F0.1	0.13	0.14	0.15	0.17	0.2	0.25	0.36
Fmax	0.36	0.44	0.59	0.87	N/A	N/A	N/A
YPRmax	6.02	6.12	6.21	6.28	N/A	N/A	N/A
F40% MSP	0.10	0.11	0.13	0.16	0.21	0.32	0.57
F30% MSP	0.13	0.15	0.18	0.23	0.32	0.52	0.99
M	0.07	0.07	0.07	0.07	0.07	0.07	0.07
Tmax	50	50	50	50	50	50	50
Z at F40%	0.17	0.18	0.20	0.23	0.28	0.39	0.64
Z at F30%	0.20	0.22	0.25	0.3	0.39	0.59	1.06
U at F40%	0.09	0.10	0.11	0.14	0.18	0.27	0.42
U at F30%	0.12	0.13	0.16	0.20	0.26	0.39	0.61

Table 3.1.8. Reference points from yield per recruit analysis for Arkansas River, Arkansas (M = 0.14).

Ref Point	Minimum size, inches						
	32	33	34	35	36	37	38
F0.1	0.21	0.23	0.25	0.28	0.33	0.43	0.60
Fmax	N/A	N/A	N/A	N/A	N/A	N/A	N/A
YPRmax	N/A	N/A	N/A	N/A	N/A	N/A	N/A
F40% MSP	0.12	0.14	0.17	0.22	0.32	0.54	1.10
F30% MSP	0.16	0.19	0.24	0.33	0.51	0.94	2.09
M	0.14	0.14	0.14	0.14	0.14	0.14	0.14
Tmax	30	30	30	30	30	30	30
Z at F40%	0.26	0.28	0.31	0.36	0.46	0.68	1.24
Z at F30%	0.30	0.33	0.38	0.47	0.65	1.08	2.23
U at F40%	0.10	0.12	0.14	0.19	0.26	0.39	0.63
U at F30%	0.14	0.16	0.20	0.26	0.38	0.57	0.84

Table 3.1.9. Reference points from yield per recruit analysis for Arkansas River, Arkansas (M = 0.20).

Ref Point	Minimum size, inches						
	32	33	34	35	36	37	38
F0.1	0.31	0.34	0.38	0.51	0.52	0.68	1.41
Fmax	N/A	N/A	N/A	N/A	N/A	N/A	N/A
YPRmax	N/A	N/A	N/A	N/A	N/A	N/A	N/A
F40% MSP	0.14	0.17	0.21	0.37	0.47	0.86	2.85
F30% MSP	0.20	0.24	0.31	0.55	0.75	1.52	6
M	0.20	0.20	0.20	0.20	0.20	0.20	0.20
Tmax	30	30	30	30	30	30	30
Z at F40%	0.34	0.37	0.41	0.57	0.67	1.06	3.05
Z at F30%	0.40	0.44	0.51	0.75	0.95	1.72	6.2
U at F40%	0.12	0.14	0.17	0.29	0.34	0.53	0.89
U at F30%	0.16	0.19	0.24	0.39	0.49	0.72	0.97

Table 3.1.10. Reference points from yield per recruit analysis for Grand Lake, Oklahoma (M = 0.14)

Ref Point	Minimum size, inches						
	32	33	34	35	36	37	38
F0.1	0.19	0.2	0.21	0.22	0.23	0.25	0.27
Fmax	0.89	N/A	N/A	N/A	N/A	N/A	N/A
YPRmax	4.91	N/A	N/A	N/A	N/A	N/A	N/A
F40% MSP	0.10	0.11	0.12	0.13	0.15	0.17	0.21
F30% MSP	0.14	0.15	0.17	0.18	0.21	0.25	0.32
M	0.14	0.14	0.14	0.14	0.14	0.14	0.14
Tmax	30	30	30	30	30	30	30
Z at F40%	0.24	0.25	0.26	0.27	0.29	0.31	0.35
Z at F30%	0.28	0.29	0.31	0.32	0.35	0.39	0.46
U at F40%	0.09	0.10	0.11	0.11	0.13	0.15	0.18
U at F30%	0.12	0.13	0.14	0.16	0.18	0.21	0.26

Table 3.1.11. Reference points from yield per recruit analysis for Grand Lake, Oklahoma (M = 0.20)

Ref Point	Minimum size, inches						
	32	33	34	35	36	37	38
F0.1	0.29	0.3	0.32	0.34	0.36	0.39	0.43
Fmax	N/A	N/A	N/A	N/A	N/A	N/A	N/A
YPRmax	N/A	N/A	N/A	N/A	N/A	N/A	N/A
F40% MSP	0.13	0.14	0.15	0.17	0.2	0.24	0.32
F30% MSP	0.18	0.19	0.21	0.24	0.28	0.35	0.47
M	0.20	0.20	0.20	0.20	0.20	0.20	0.20
Tmax	21	21	21	21	21	21	21
Z at F40%	0.33	0.34	0.35	0.37	0.4	0.44	0.52
Z at F30%	0.38	0.39	0.41	0.44	0.48	0.55	0.67
U at F40%	0.11	0.12	0.13	0.14	0.16	0.2	0.25
U at F30%	0.15	0.16	0.17	0.19	0.22	0.27	0.34

Table 3.1.12. Reference points from yield per recruit analysis for Lower Mississippi River (M = 0.14)

Ref Point	Minimum size, inches						
	32	33	34	35	36	37	38
F0.1	0.21	0.22	0.23	0.25	0.27	0.3	0.34
Fmax	N/A	N/A	N/A	N/A	N/A	N/A	N/A
YPRmax	N/A	N/A	N/A	N/A	N/A	N/A	N/A
F40% MSP	0.10	0.11	0.12	0.14	0.16	0.21	0.28
F30% MSP	0.13	0.15	0.17	0.19	0.24	0.31	0.45
M	0.14	0.14	0.14	0.14	0.14	0.14	0.14
Tmax	30	30	30	30	30	30	30
Z at F40%	0.24	0.25	0.26	0.28	0.3	0.35	0.42
Z at F30%	0.27	0.29	0.31	0.33	0.38	0.45	0.59
U at F40%	0.09	0.09	0.10	0.12	0.14	0.17	0.23
U at F30%	0.12	0.13	0.14	0.16	0.20	0.25	0.34

Table 3.1.13. Reference points from yield per recruit analysis for Alabama River (M = 0.25)

Ref Point	Minimum size, inches						
	32	33	34	35	36	37	38
F0.1	0.42	0.44	0.47	0.51	0.56	0.63	0.74
Fmax	N/A	N/A	N/A	N/A	N/A	N/A	N/A
YPRmax	N/A	N/A	N/A	N/A	N/A	N/A	N/A
F40% MSP	0.19	0.22	0.26	0.31	0.40	0.56	0.86
F30% MSP	0.27	0.31	0.37	0.47	0.63	0.95	1.64
M	0.25	0.25	0.25	0.25	0.25	0.25	0.25
Tmax	17	17	17	17	17	17	17
Z at F40%	0.44	0.47	0.51	0.56	0.65	0.81	1.11
Z at F30%	0.52	0.56	0.62	0.72	0.88	1.2	1.89
U at F40%	0.16	0.17	0.20	0.24	0.30	0.38	0.52
U at F30%	0.21	0.24	0.28	0.33	0.42	0.55	0.74

Table 3.1.14. Fishing mortality values that maximize egg per recruit (EPR) and yield per recruit (YPR) for Kentucky lake at various minimum sizes.

Variable	Minimum size, inches						
	32	33	34	35	36	37	38
EPR	0.49	0.58	0.70	0.88	0.88	N/A	N/A
YPR	0.44	0.51	0.6	0.72	0.91	N/A	N/A

Table 3.8.1. Comparison of fishing mortality rates to $F_{40\%}$ reference points for all systems with total mortality rate estimates from Section 2.10.

System	Years	Z	M	F	$F_{40\%}$	$F/F_{40\%}$
Lake Francis Case	1995-2005	0.18	0.07	0.11	0.06	1.78
Barclay Reservoir (TN)	2008-2012	0.53	0.14	0.39	0.09	4.28
Cheatham Reservoir (TN)	2008-2012	0.59	0.14	0.45	0.09	4.98
Mississippi (TN)	2008-2012	0.89	0.14	0.75	0.09	8.36
Kentucky Lake (TN)	2008-2012	0.30	0.14	0.16	0.09	1.77
Cumberland Reservoir (TN)	2010-2012	0.88	0.14	0.74	0.09	8.19
Sunflower River (MS)	2010-2012	1.02	0.25	0.77	0.56	1.37
Mississippi (MS)	2008-2012	0.67	0.14	0.53	0.12	4.41
Moon Lake (MS)	2010-2011	NA	0.25	NA	NA	NA
4 Mile Lake (MS)	2010-2012	0.64	0.25	0.39	0.56	0.69
Delta Zone (MS)	2010-2012	0.54	0.25	0.29	0.56	0.51
Arkansas River (AR)	2003-2004	1.35	0.14	1.21	0.21	5.76
Mississippi River (AR)	2011	0.50	0.14	0.36	0.13	2.73
Mississippi River (MO)	2011	0.50	0.14	0.36	0.13	2.76

7. Figures
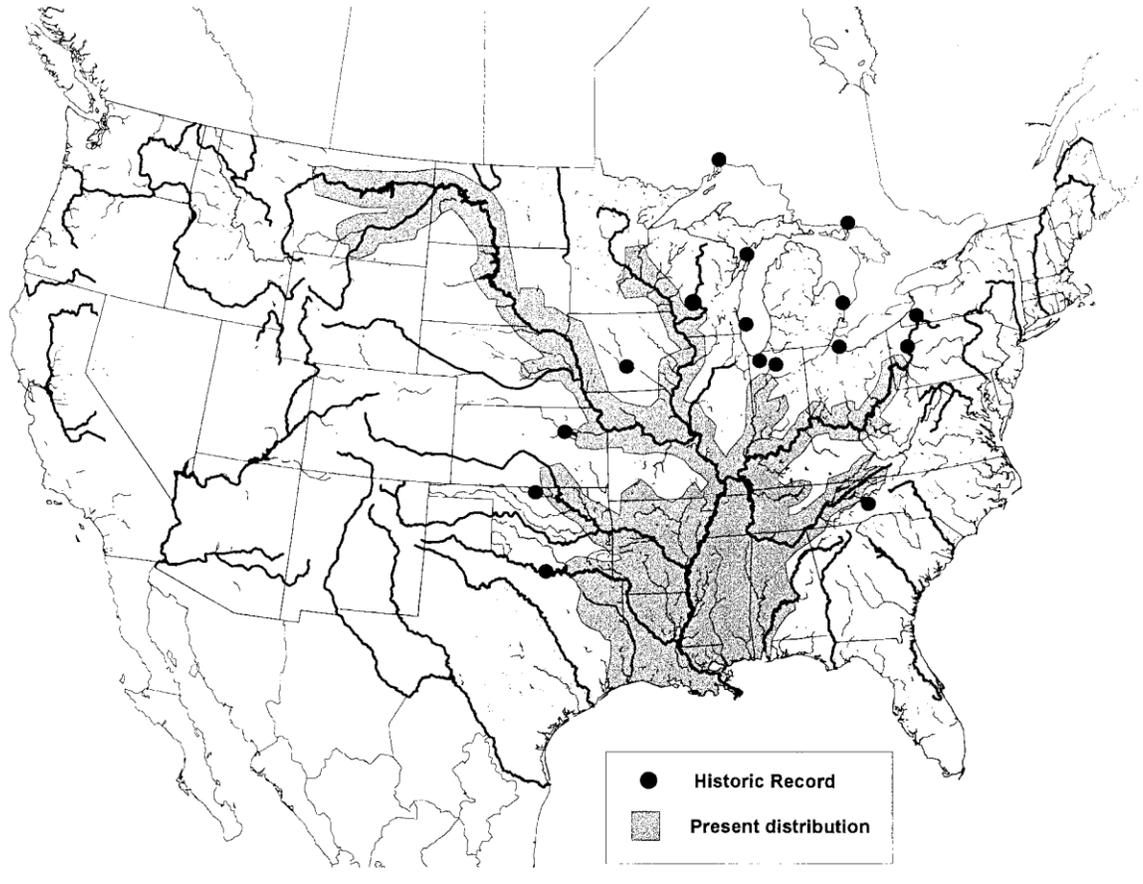
Figure 2.1.1. Distribution of Paddlefish (*Polyodon spathula*, Polyodontidae) in North America (adapted from Jennigns and Zigler, 2000 and Carlson and Bonislawsky, 1981).
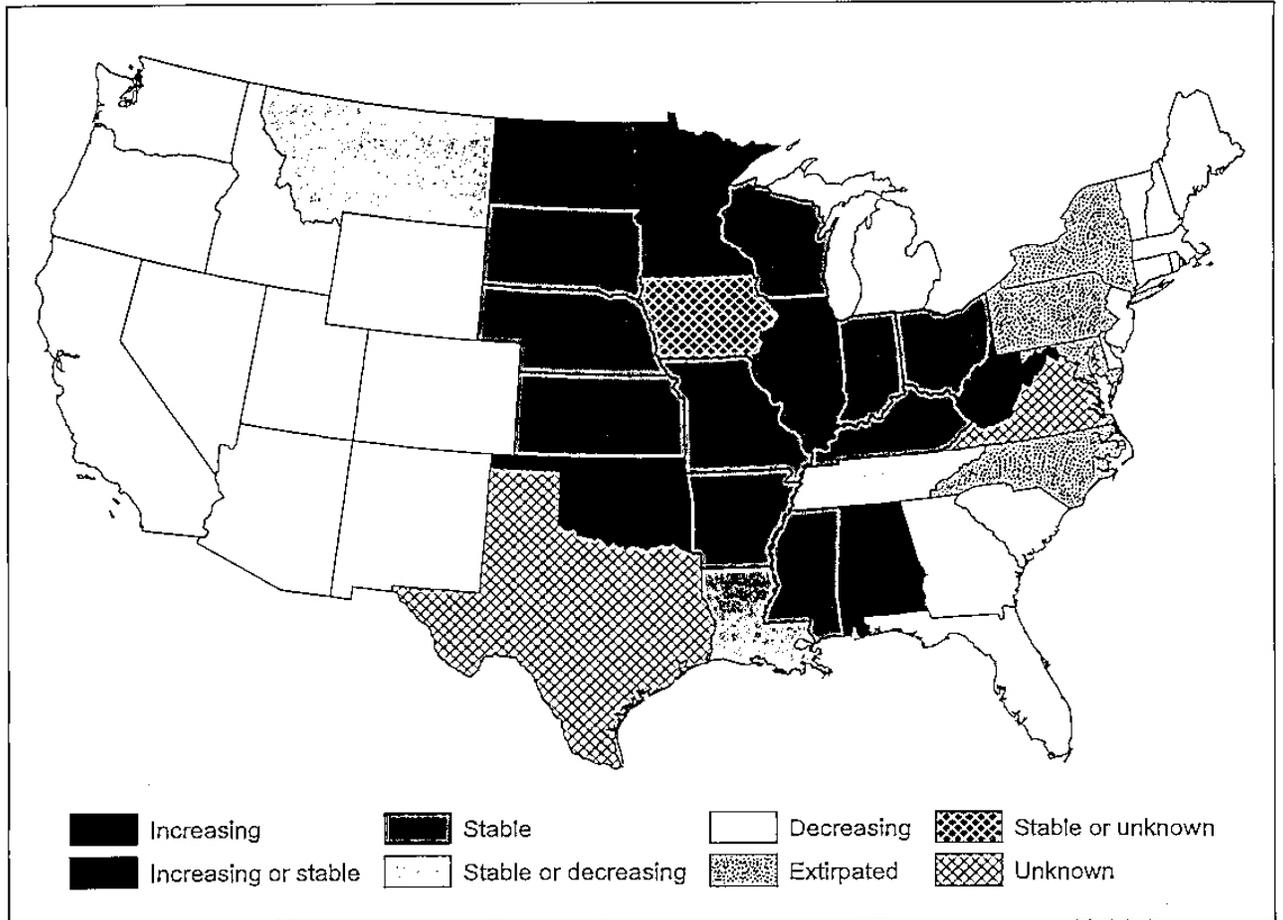
Figure 2.1.2. Status of Paddlefish stocks in the United States based on a 2006 survey of state and federal agency personnel. . Adopted from Bettoli et al., 2009.
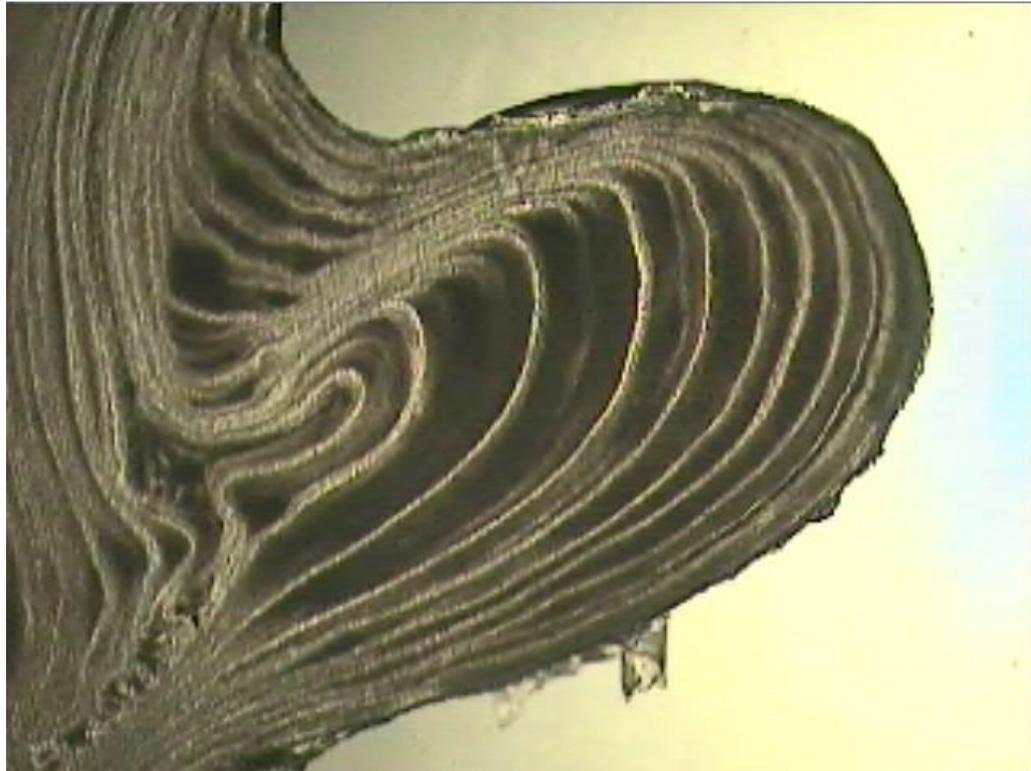
Figure 2.3.1. Photograph of a Paddlefish jaw bone cross section. Adopted from Quinn et al., 2006.
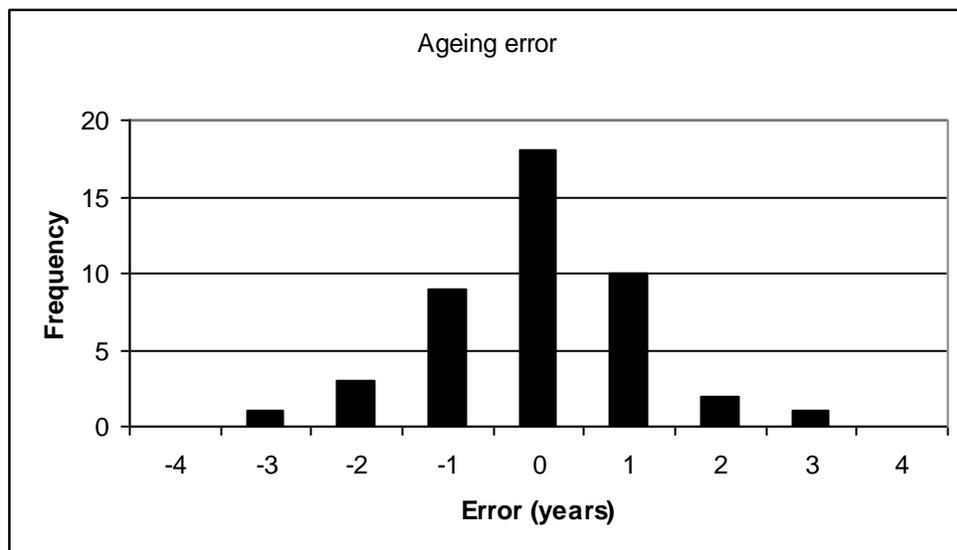
Figure 2.3.2. Histogram of the aging errors (estimated-actual age; N = 44) observed from using a double-blind aging procedure for Table Rock Lake and Harry S. Truman Lake, Missouri. Adopted from Quinn et al., 2006**.**
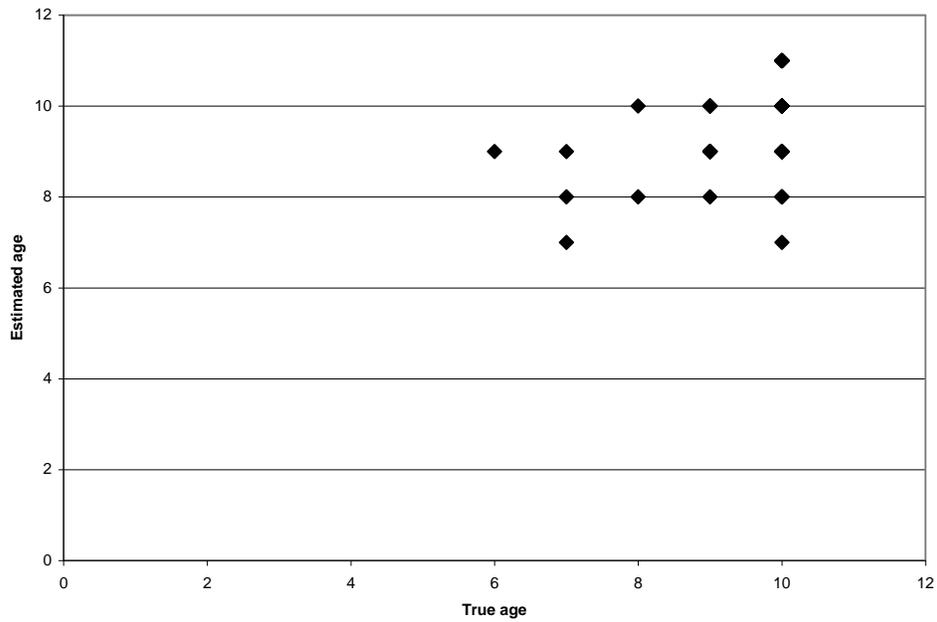
Figure 2.3.3. Scatterplot of the estimated vs. true age of Paddlefish from Harry S. Truman and Table Rock Lakes, Missouri.   Adopted from Quinn et al. (2006).
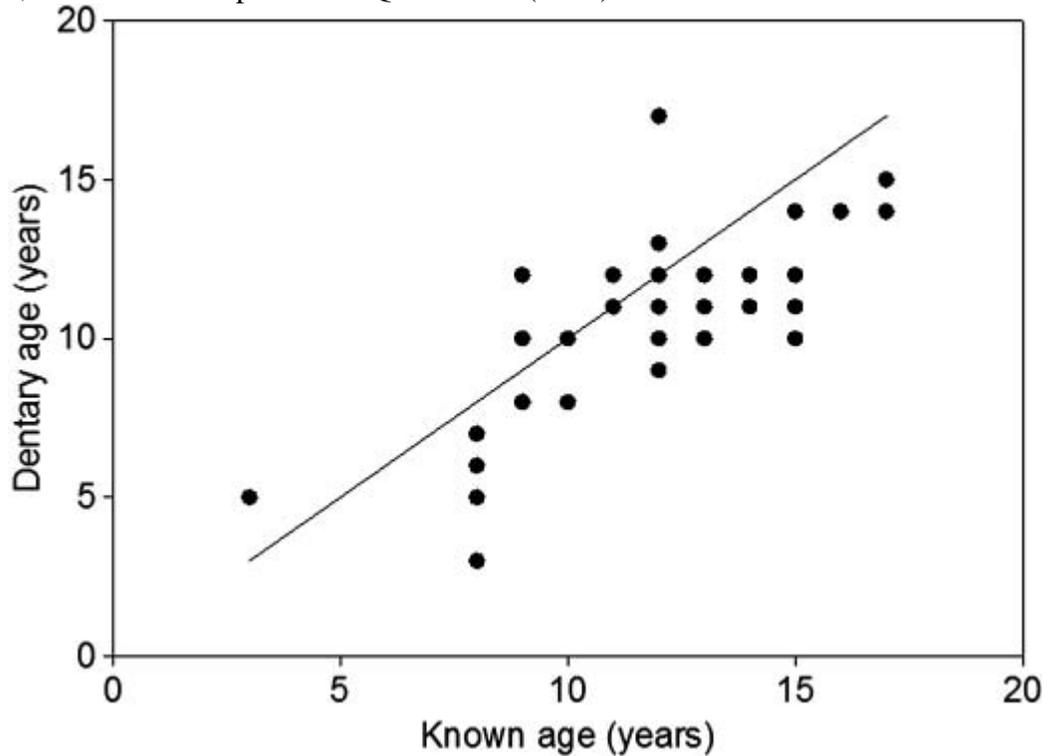
Figure 2.3.4. Lake Francis CasePaddlefish age estimates from dentary bones compared with known ages determined from coded-wire tags. The line represents a 1:1 relationship (from Pierce et al., 2011).
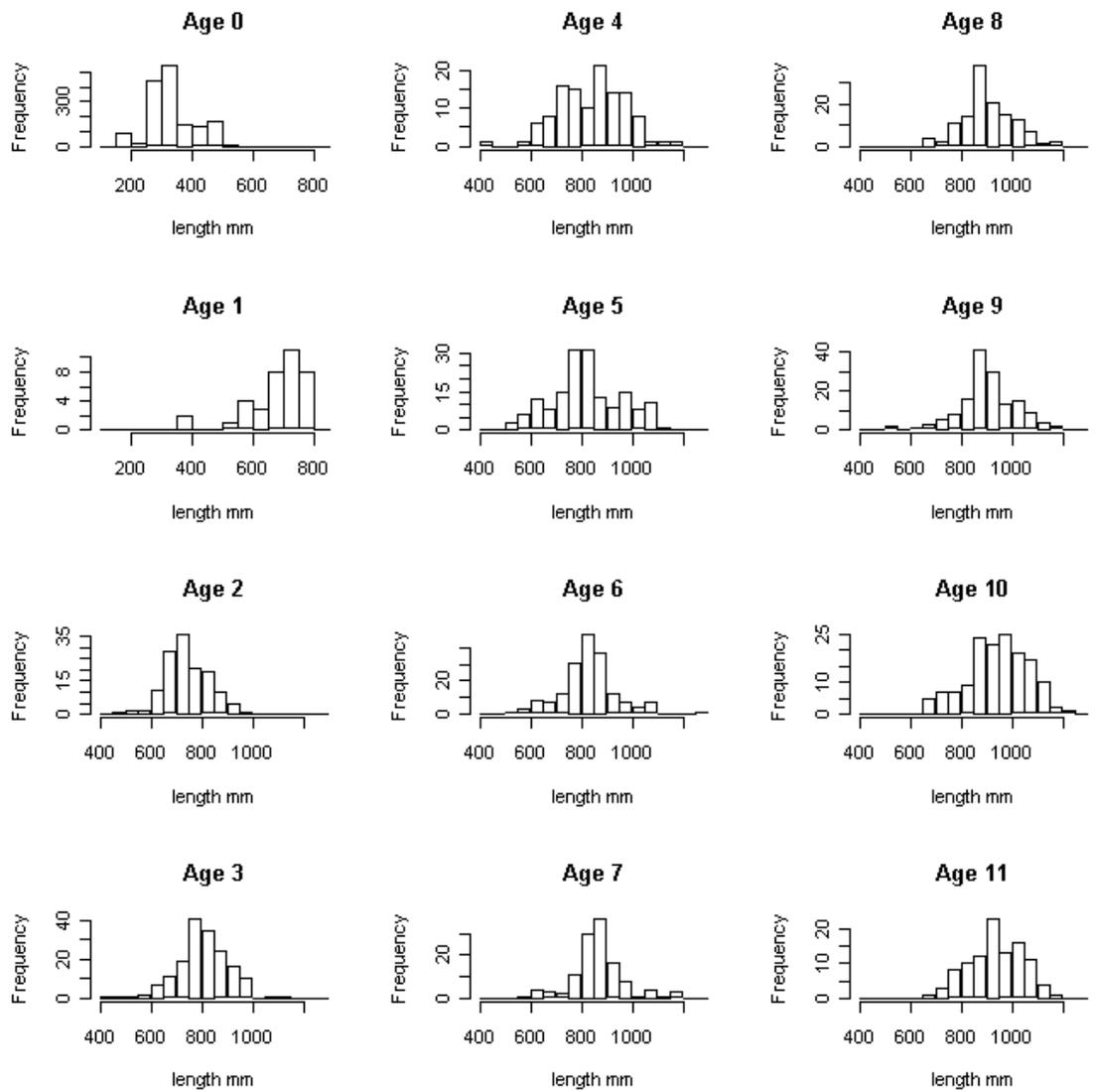
Figure 2.5.1. Histograms of size distribution by age (0 – 11), MICRA tagging data, regions combined.
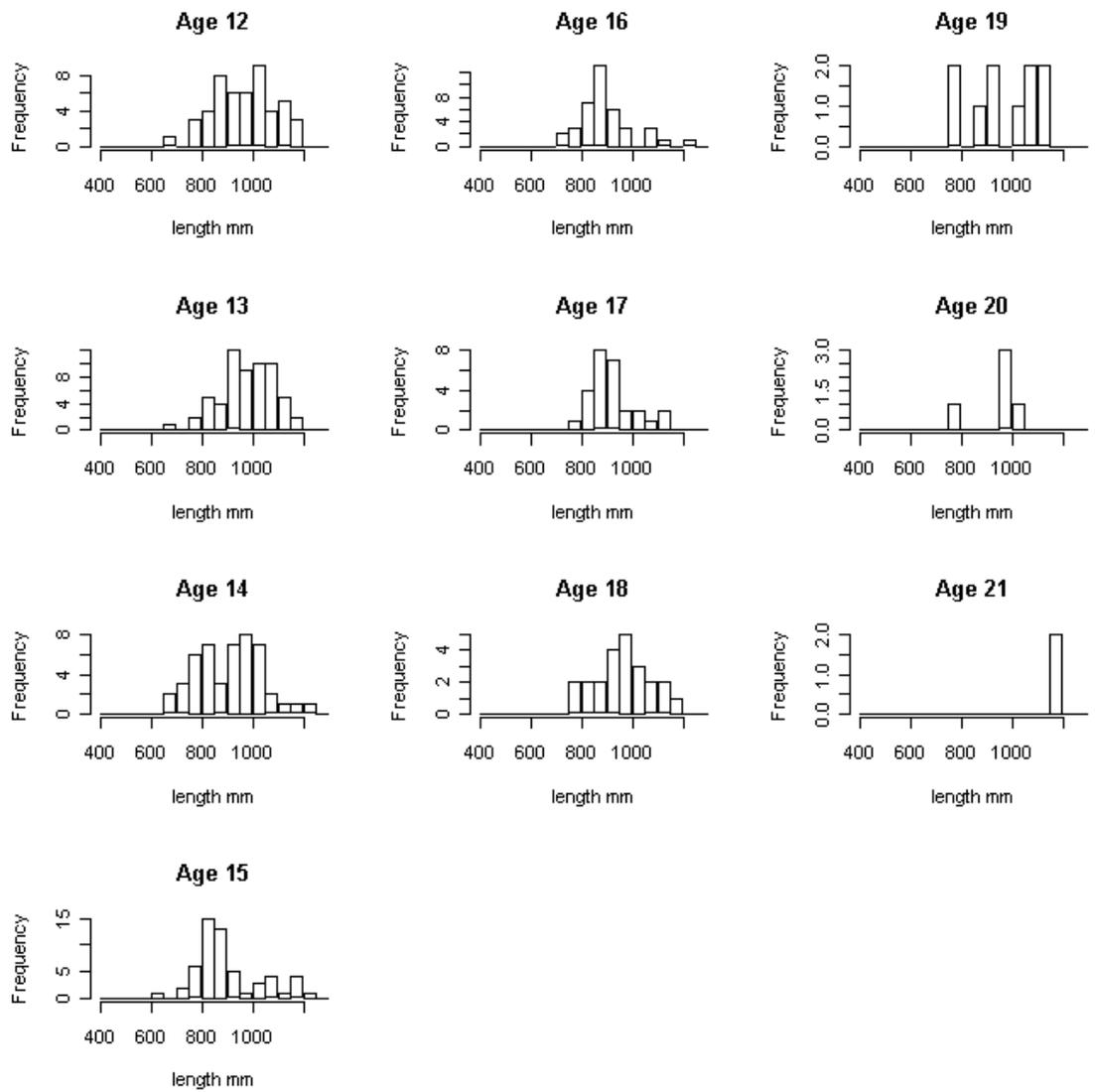
Figure 2.5.1 (continues). Histograms of size distribution by age (12 – 21), MICRA tagging data, regions combined.
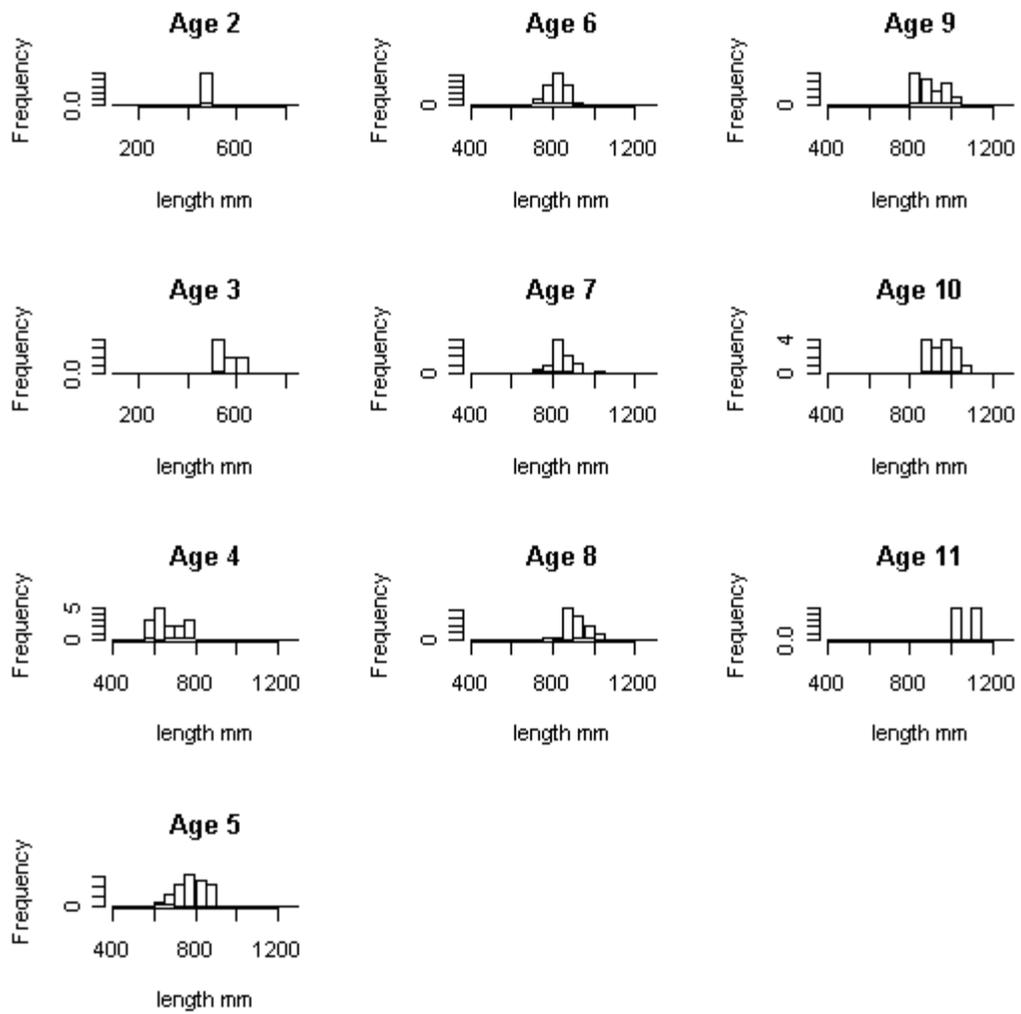
Figure 2.5.2. Histograms of Kentucky Lake Paddlefish size distribution by age $(2 - 11)$, sexes combined, data from Scholten and Bettoli, 2005.
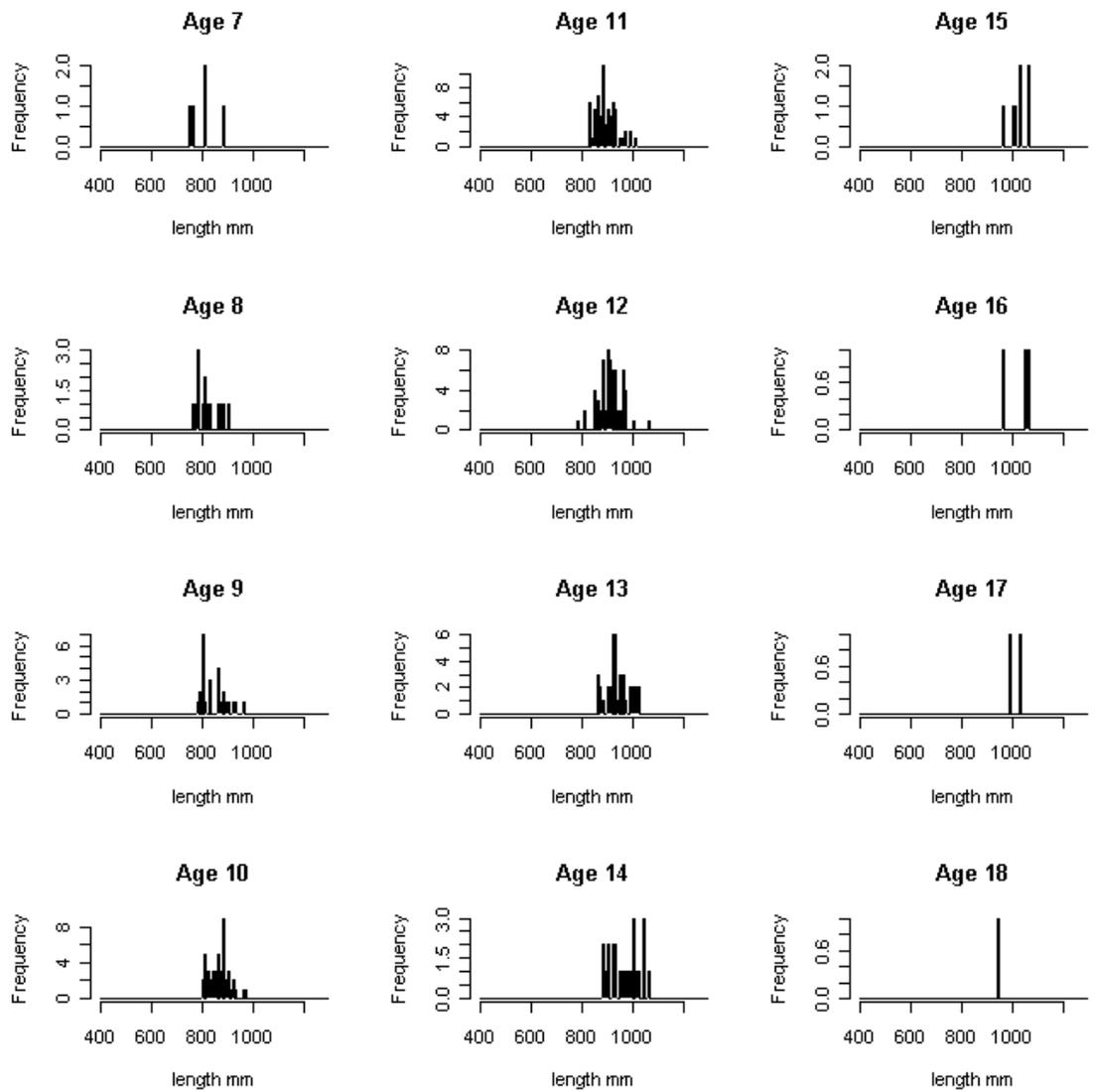
Figure 2.5.3. Histograms of of Lower Mississippi River Paddlefish size distribution by age (7– 18), sexes combined, data from Tripp et al., 2012.
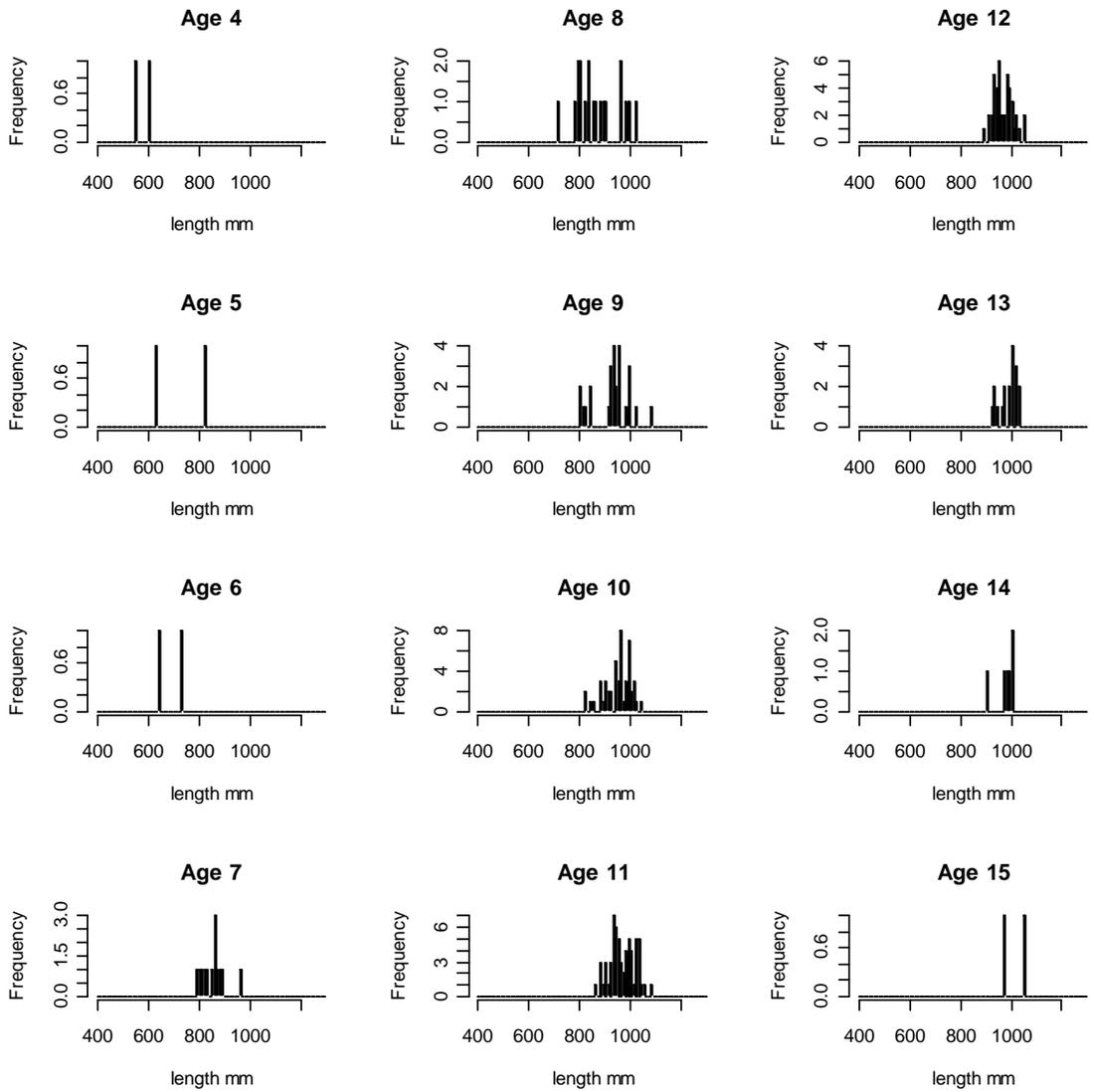
Figure 2.5.4. Histograms of Arkansas River (pools combined) female Paddlefish size distribution by age (4– 15), data from Leone et al. 2011.

MICRA tagging data
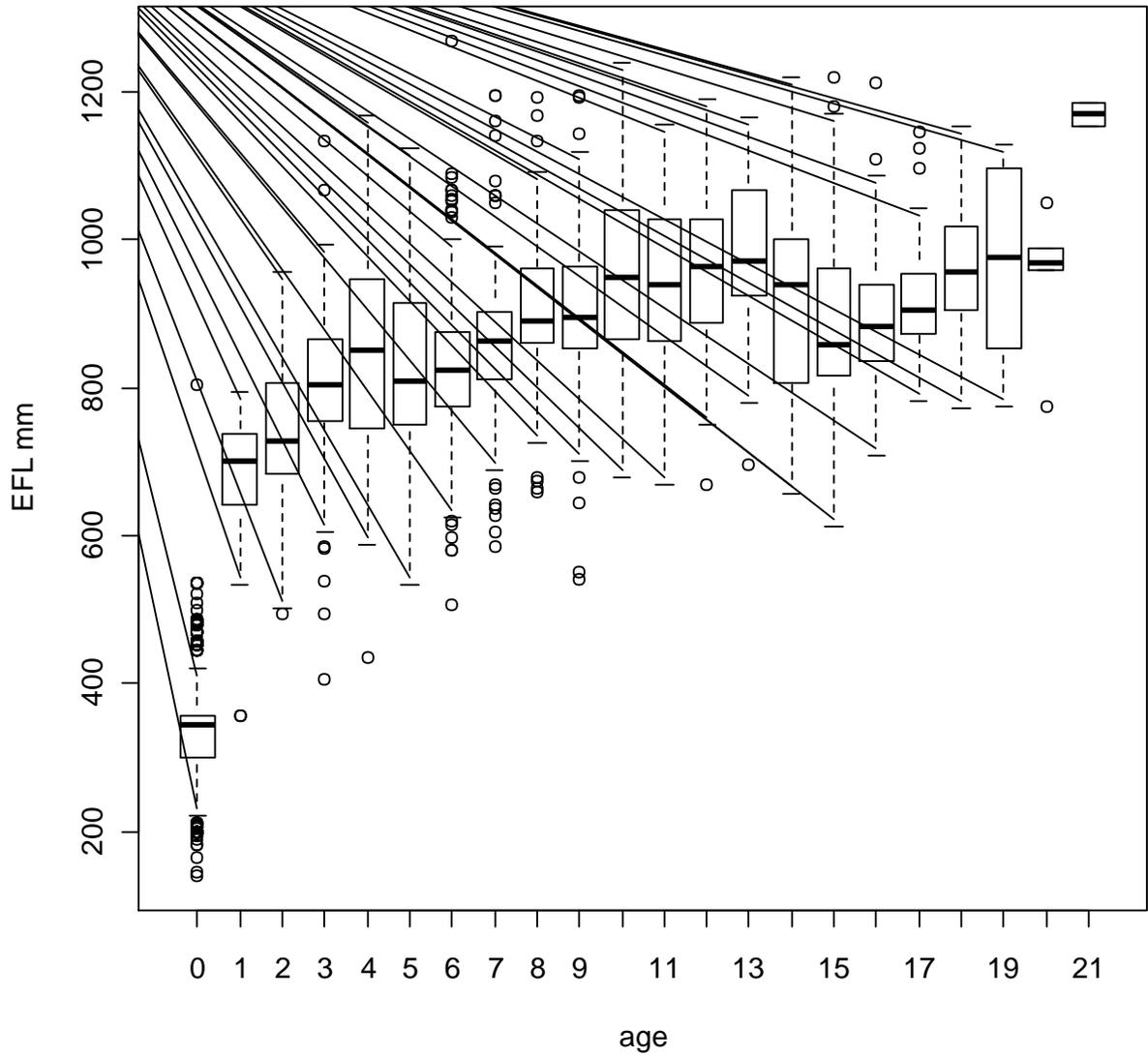
Figure 2.5.5. Boxplots of Paddlefish size distribution by age, data from   MICRA tagging data, regions combined.
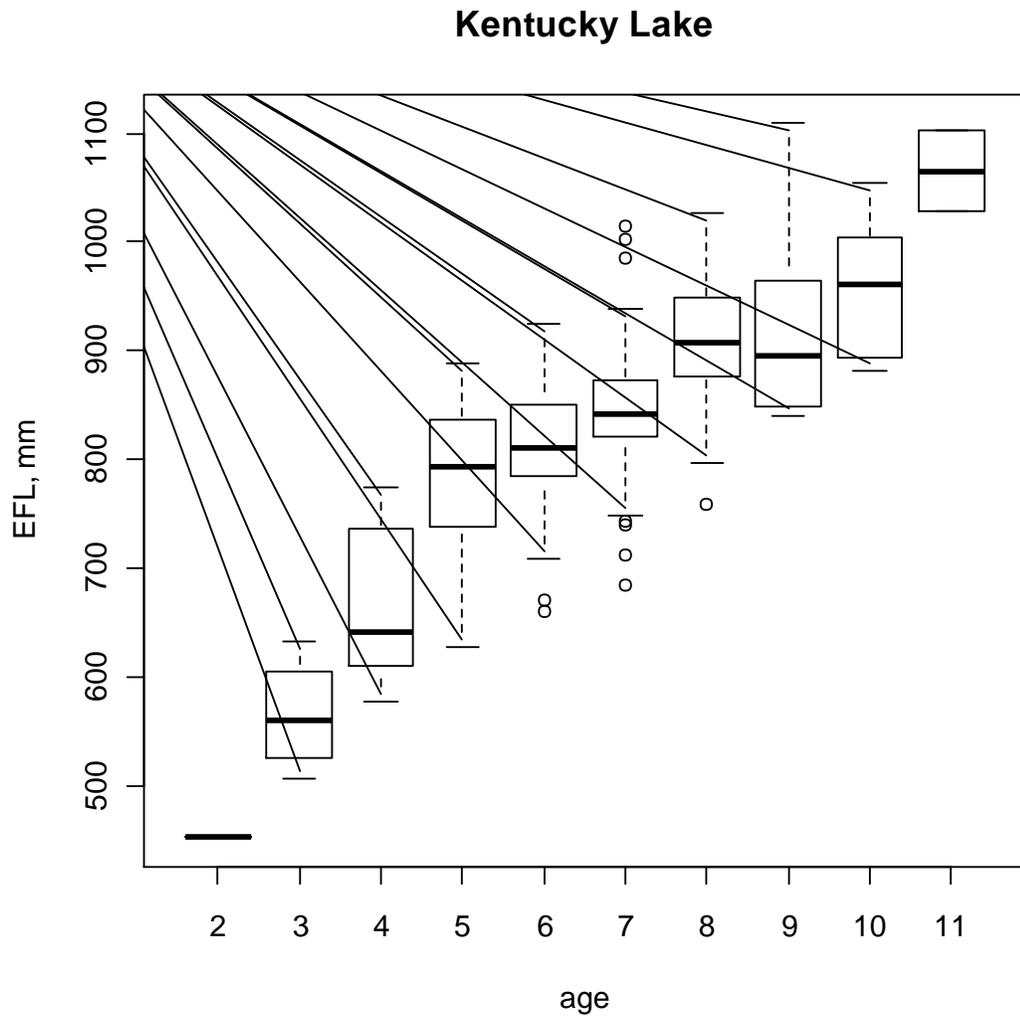
Kentucky Lake

Figure 2.5.6. Boxplots of Kentucky Lake Paddlefish size distribution by age, data from Scholten and Bettoli, 2005, sexes combined.
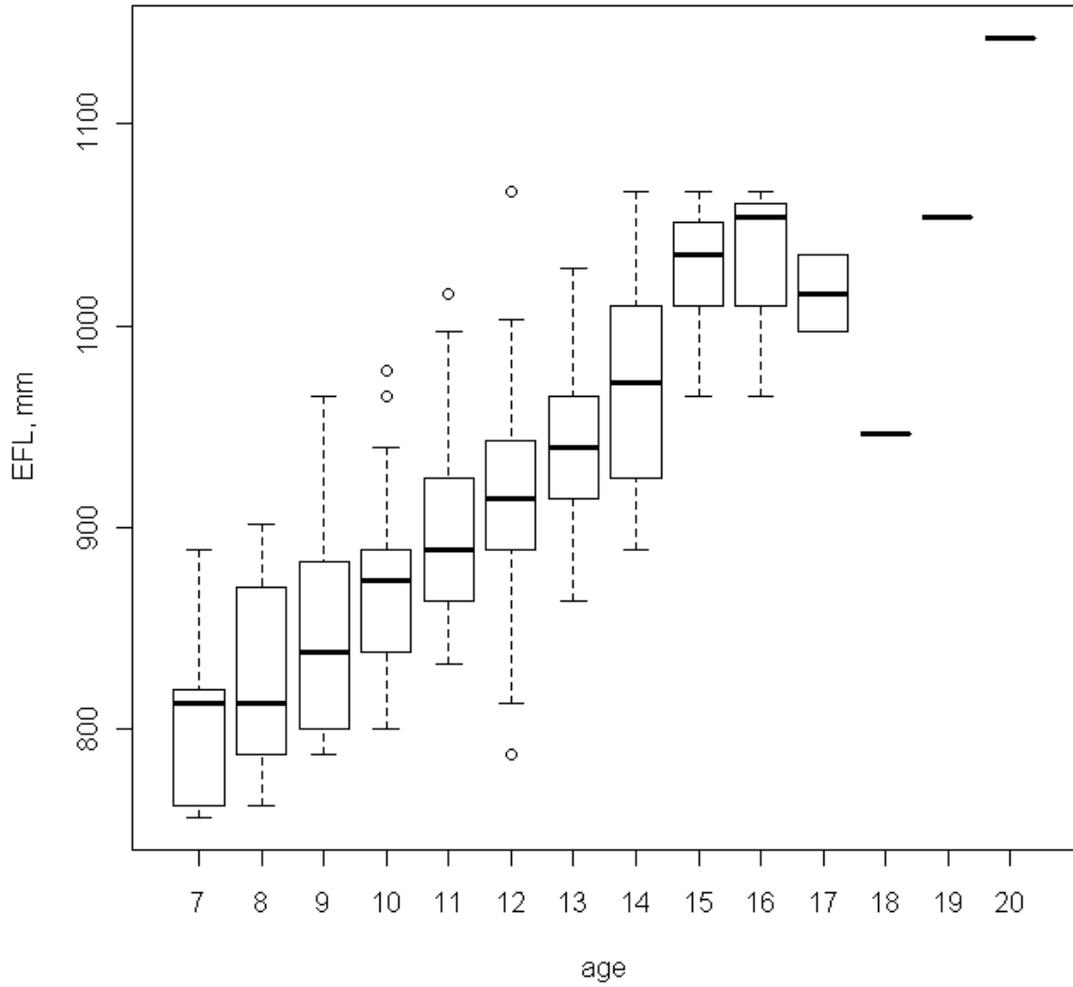
Figure 2.5.7. Boxplots Lower Mississippi River Paddlefish size distribution by age, data from Tripp et al., 2012.
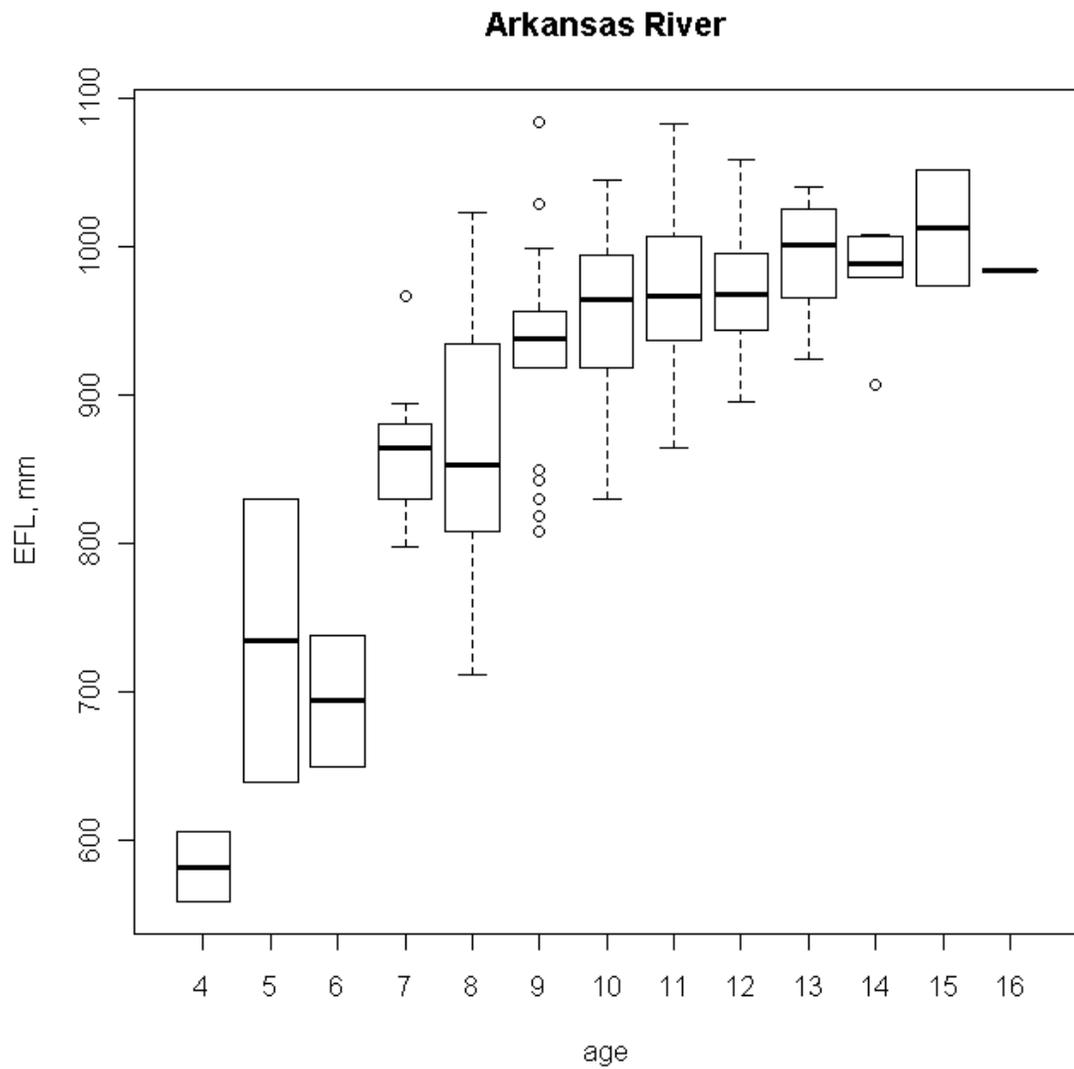
Figure 2.5.8. Boxplots for Arkansas River (pools combined) Paddlefish size distribution by age, data from Leone et al. (2011).
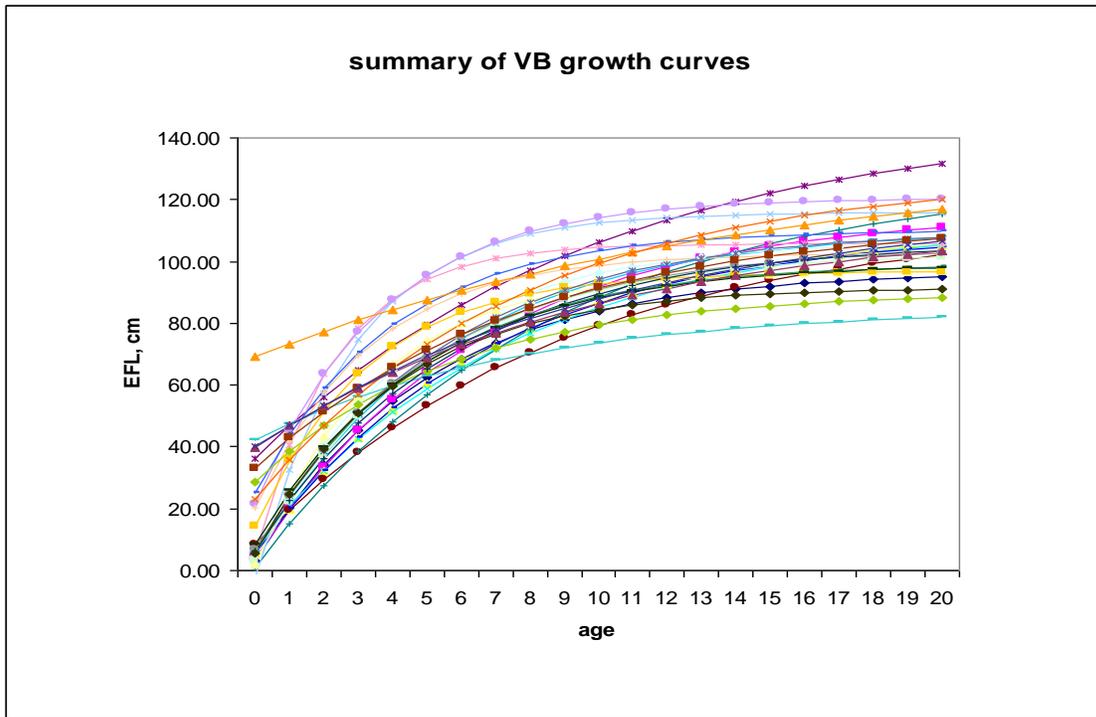
Figure 2.5.9. Family of Von Bertallanffy growth curves based on VB estimated parameters reported in literature for all regions.
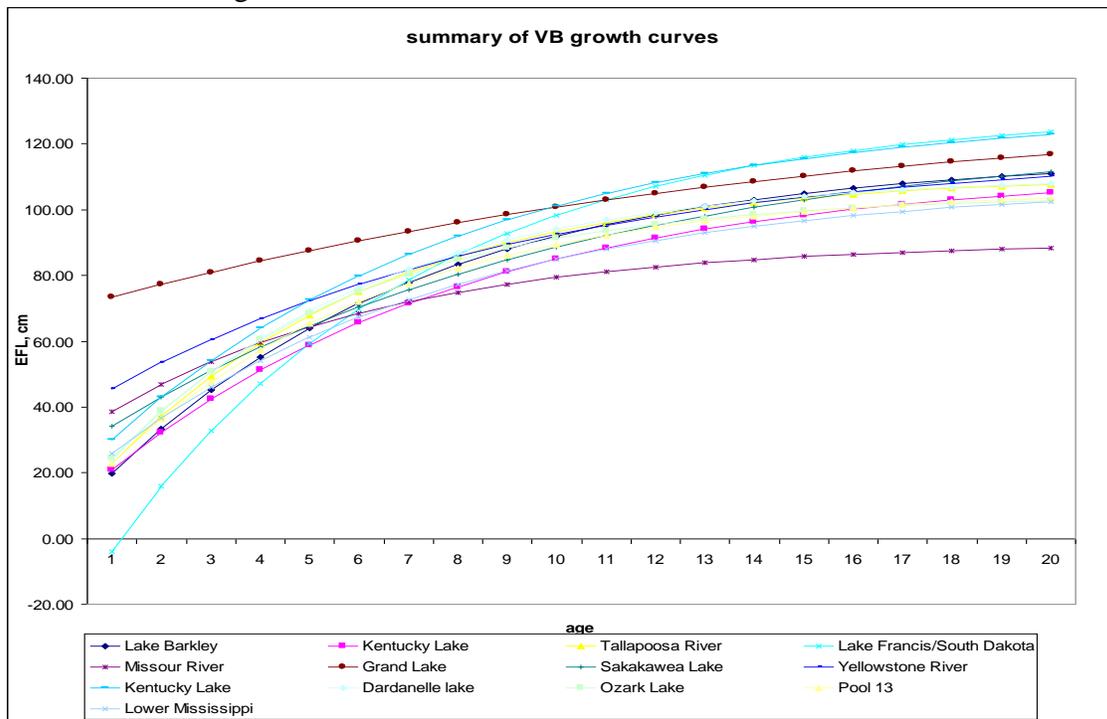
Figure 2.5.10. Family of Von Bertallanffy growth curves for female Paddlefish reported in literature for all regions.

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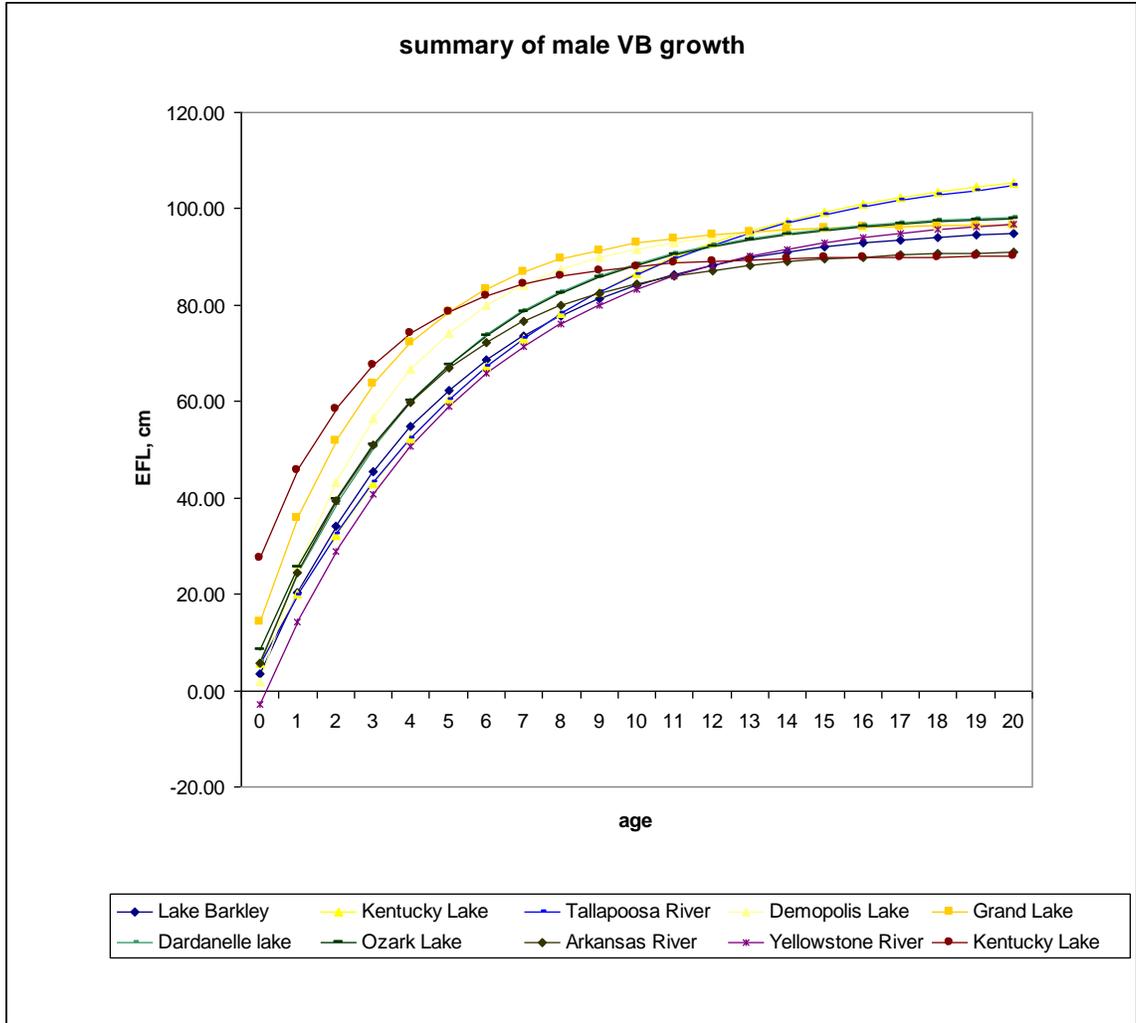
Figure 2.5.11. Family of Von Bertallanffy growth curves for male Paddlefish reported in literature for all regions.
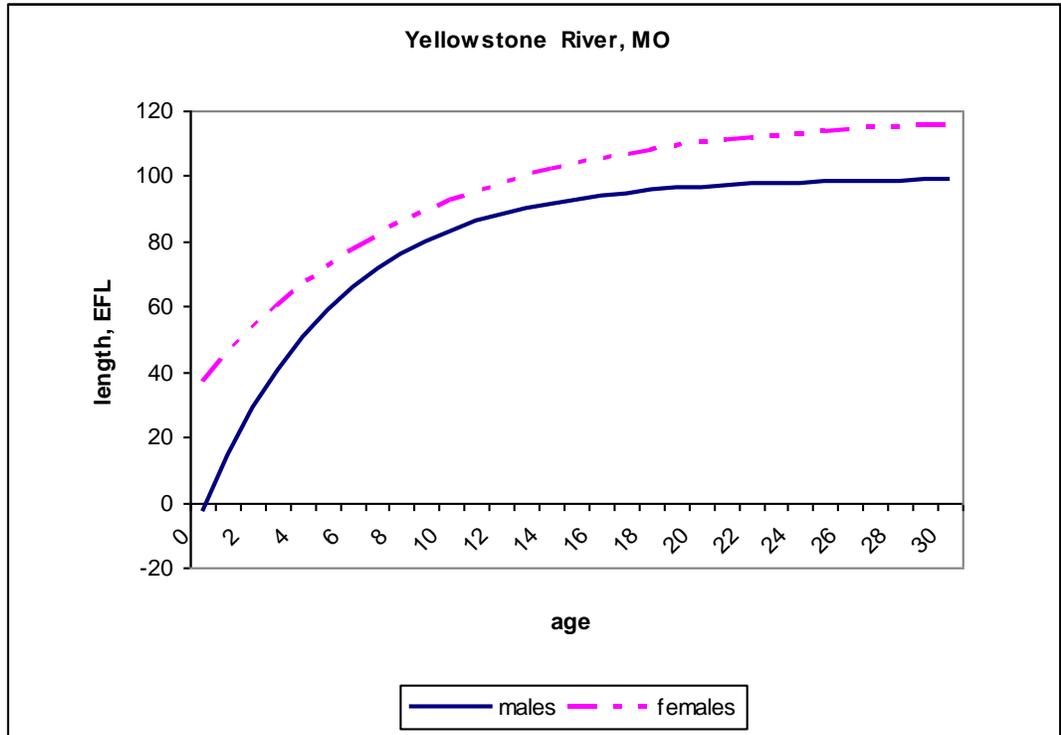
Figure 2.5.12. Growth curves for male and female Paddlefish of Yellowstone River, Montana. Growth parameters from Scarnecchia et al., 2008.
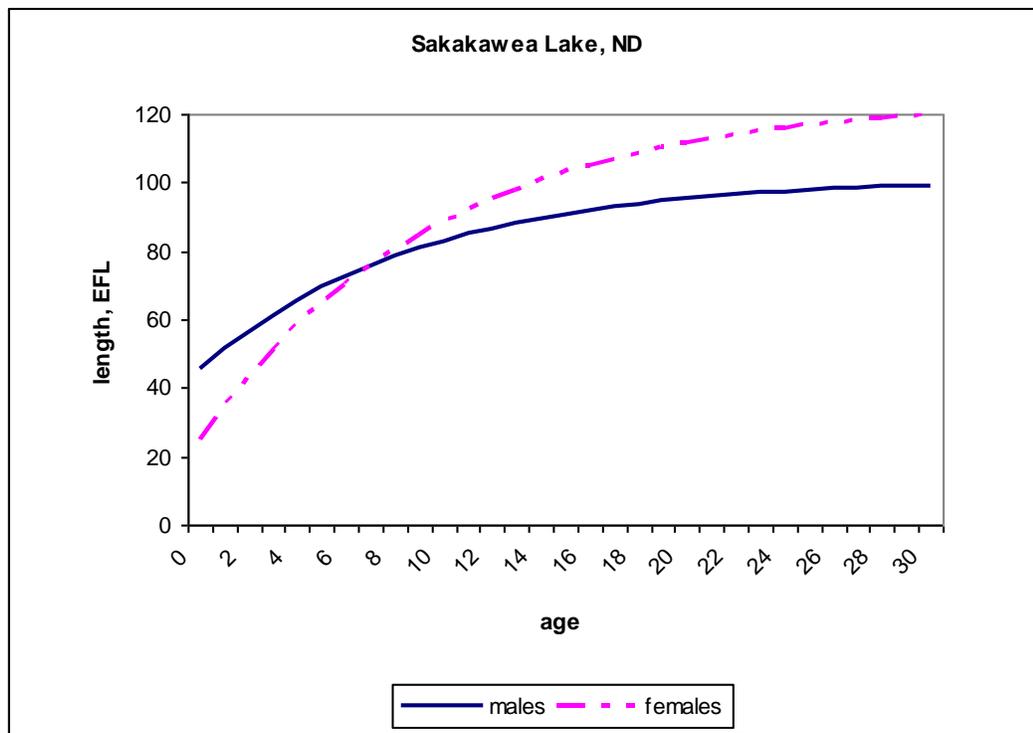
Figure 2.5.13. Growth curves for male and female Paddlefish of Sakakawea Lake, Missouri Basin, N Dakota. Growth parameters from Scarnecchia et al., 2008.
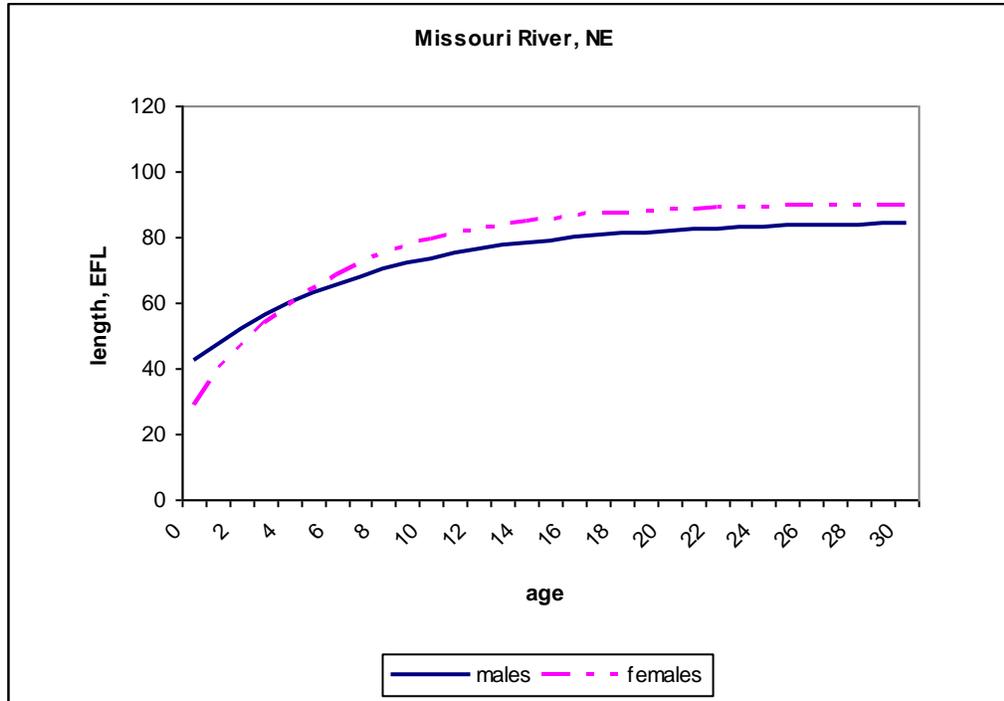
Missouri River, NE

Figure 2.5.14. Growth curves for male and female Paddlefish of Missouri River, Nebraska Growth parameters from Rosen et al., 1982

Lake Francis Case, South Dakota
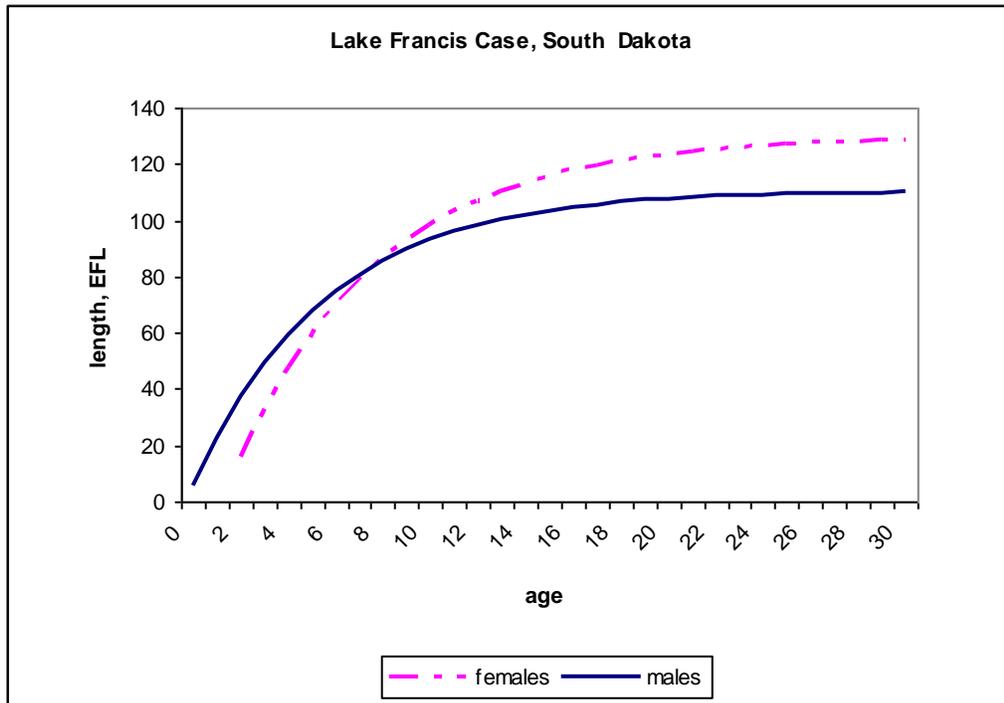
Figure 2.5.15. Growth curves for male and female Paddlefish of Lake Francis Case, Missouri River basin, S Dakota. Growth parameters from Pierce et al., 2011.

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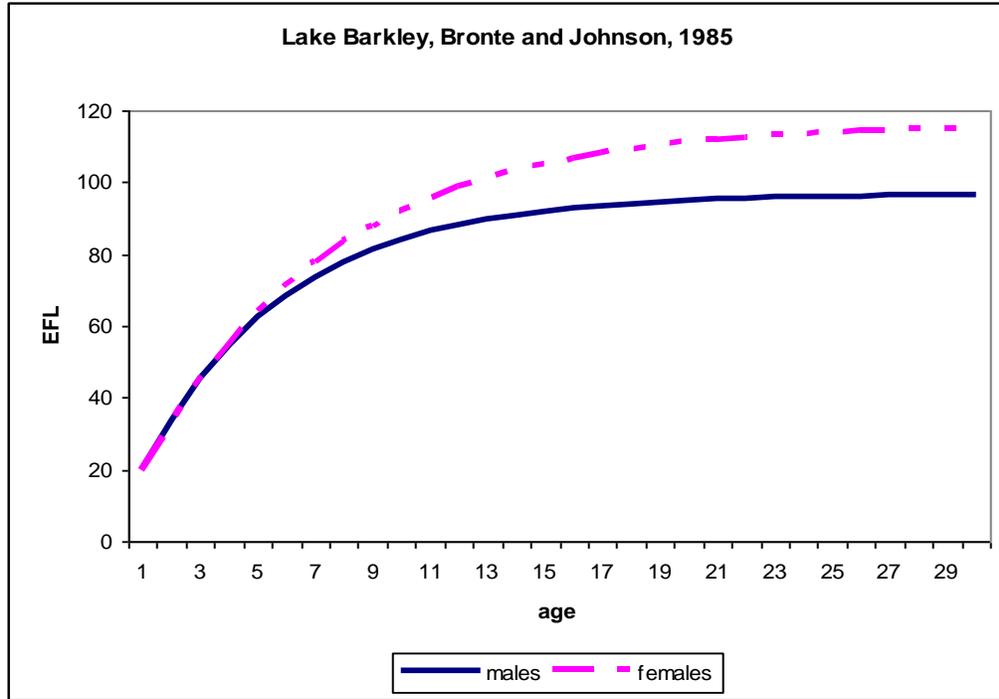
Figure 2.5.16. Growth curves for male and female Paddlefish of Lake Barkley, Cumberland River basin, Kentucky. Growth parameters from Bronte and Johnson, 1985.
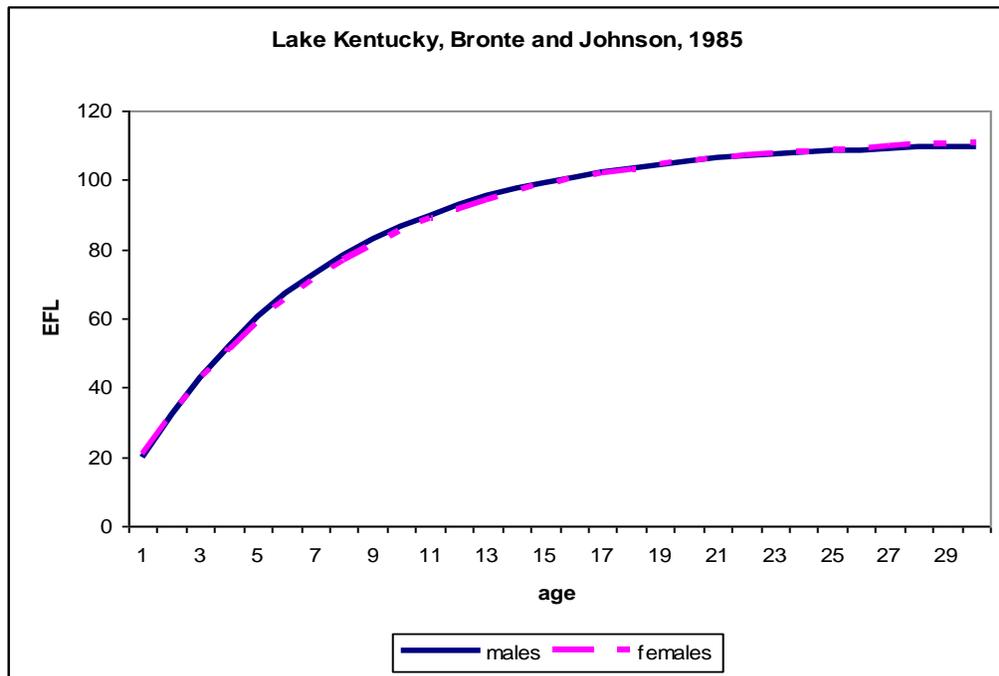
Figure 2.5.17. Growth curves for male and female Paddlefish of Lake Kentucky, Tennessee River basin, Kentucky. Growth parameters from Bronte and Johnson, 1985.
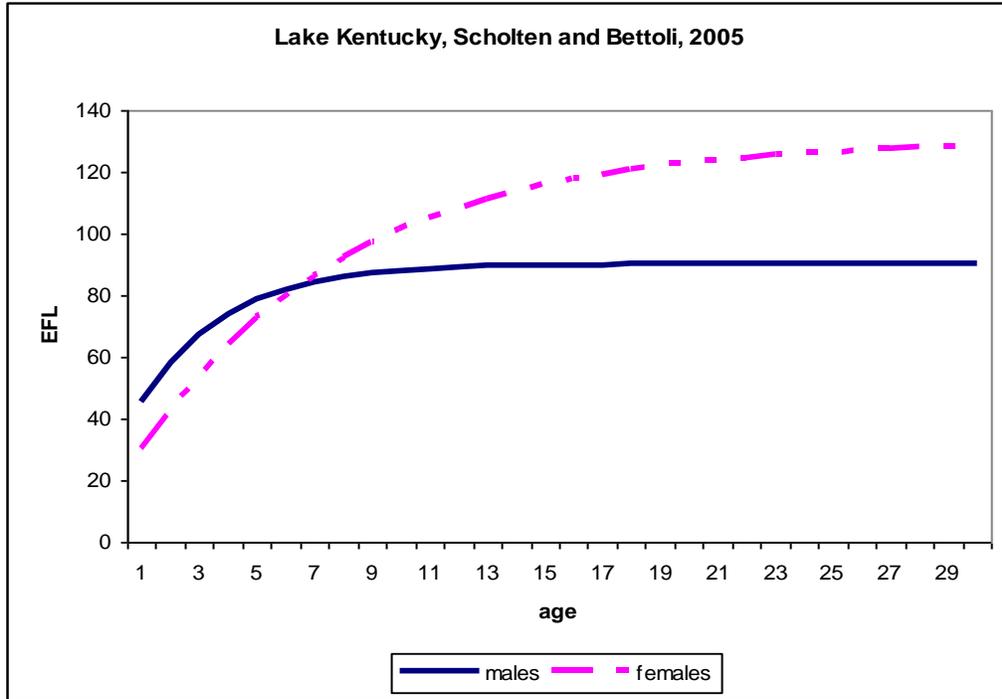
Figure 2.5.18. Growth curves for male and female Paddlefish of Lake Kentucky, Tennessee River basin, Kentucky. Growth parameters from Scholten and Bettoli, 2005.
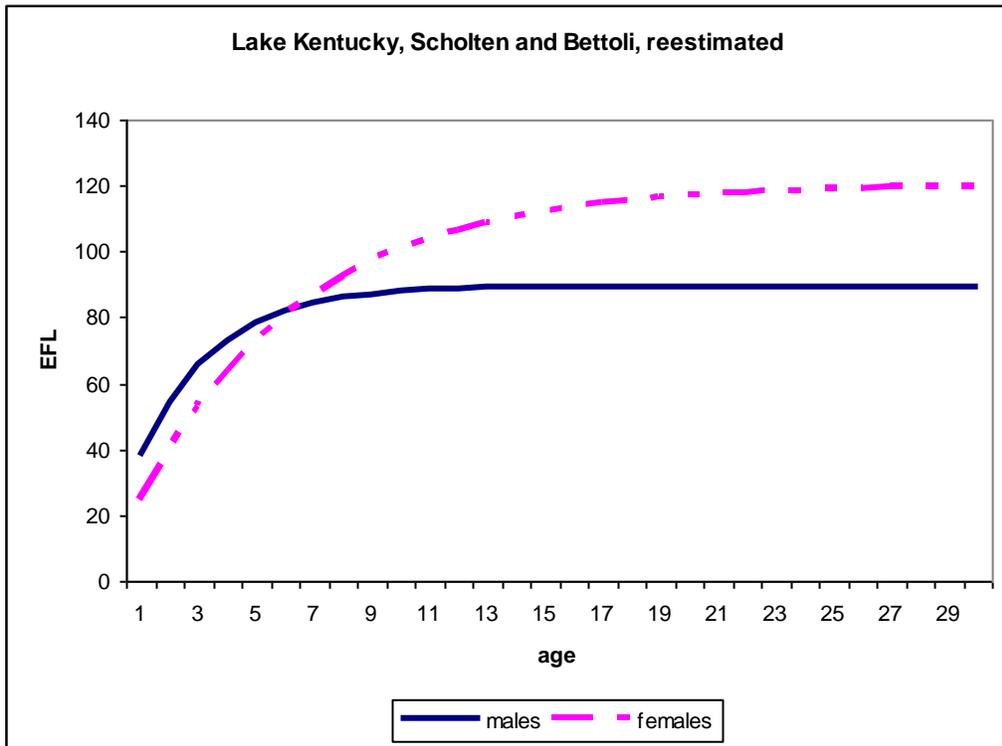
Figure 2.5.19. Growth curves for male and female Paddlefish of Lake Kentucky, Tennessee River basin, Kentucky. Growth parameters re-estimated based on data from Scholten and Bettoli, 2005.
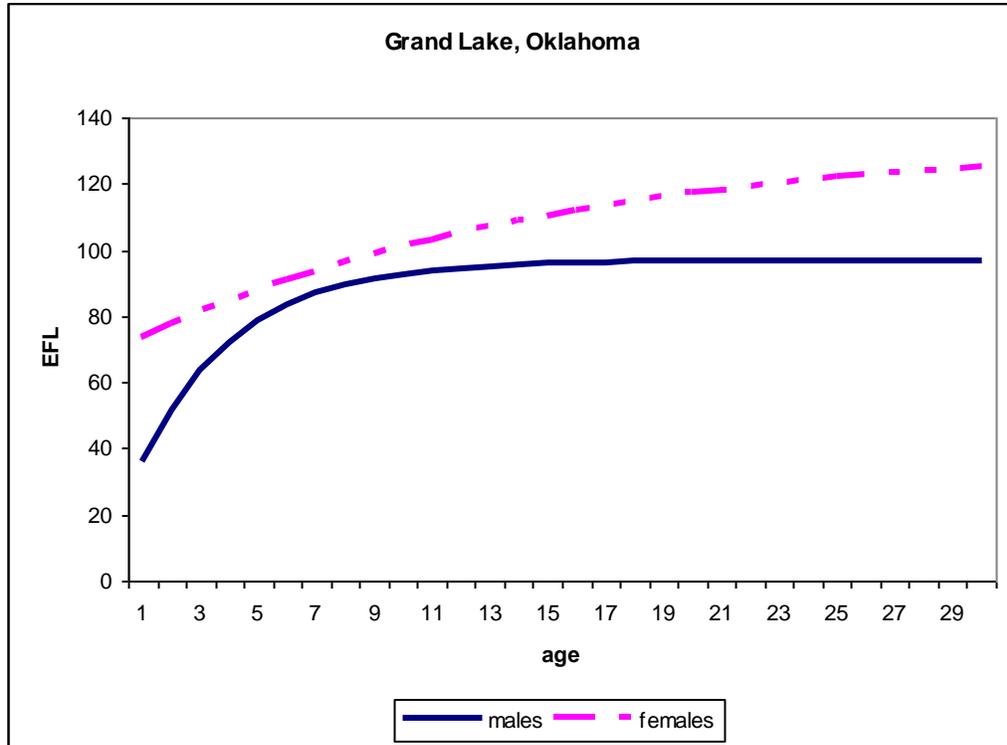
Figure 2.5.20. Growth curves for male and female Paddlefish of Grand Lake, Arkansas River basin, Oklahoma. Growth parameters from Scarnecchia et al., 2011.

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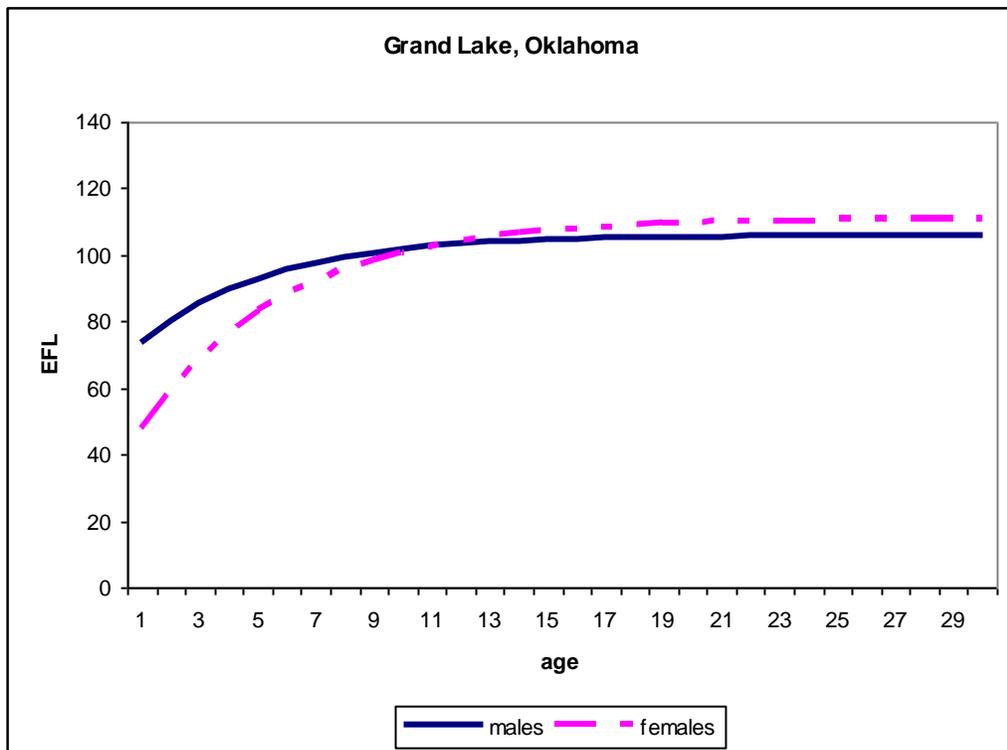
Figure 2.5.21. Growth curves for male and female Paddlefish of Grand Lake, Arkansas River basin, Oklahoma. Growth parameters re-estimated based on Scarnecchia et al., 2011.
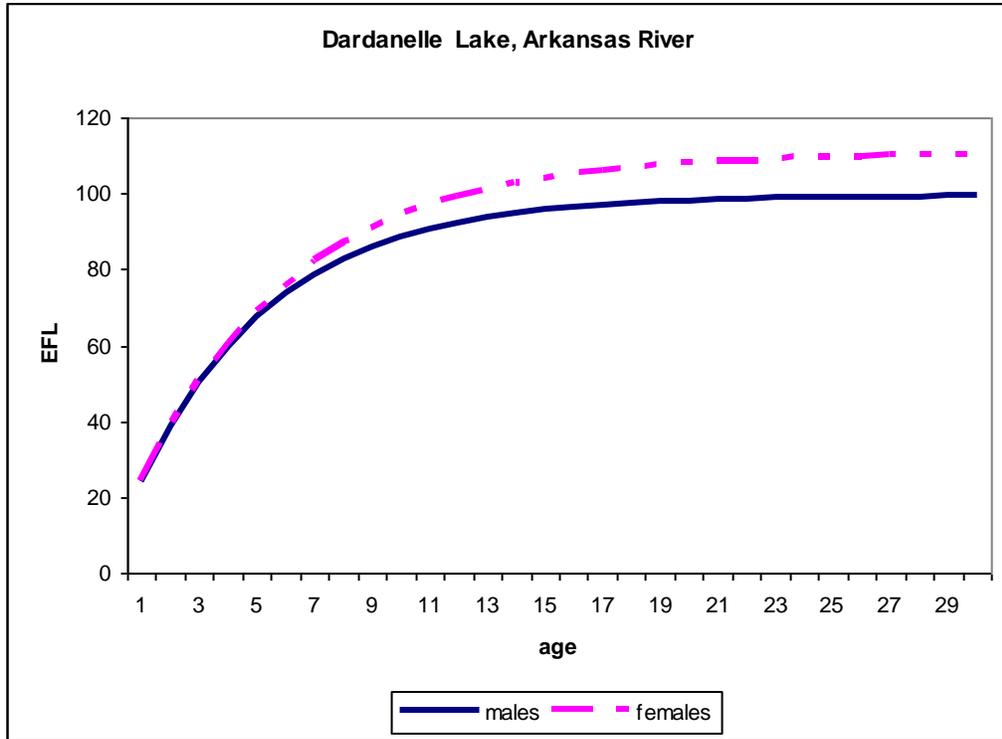
Figure 2.5.22. Growth curves for male and female Paddlefish of Dardanelle Lake, Arkansas River basin, Arkansas. Growth parameters from Leone et al., 2011.
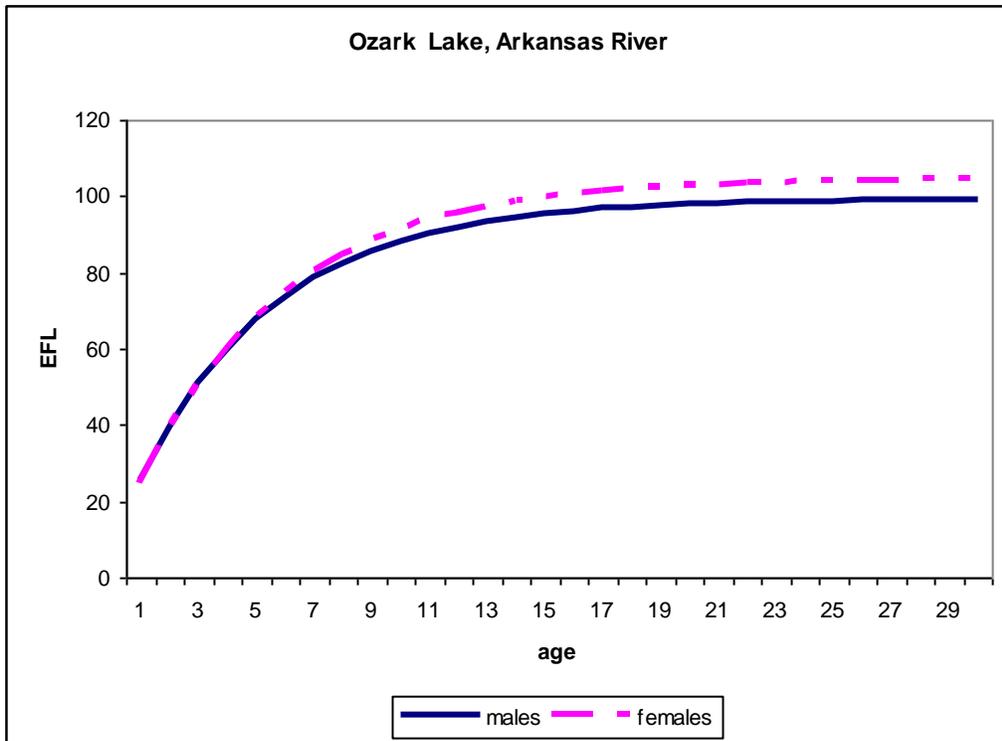
Figure 2.5.23. Growth curves for male and female Paddlefish of Ozark Lake, Arkansas River basin, Arkansas. Growth parameters from Leone et al., 2011.

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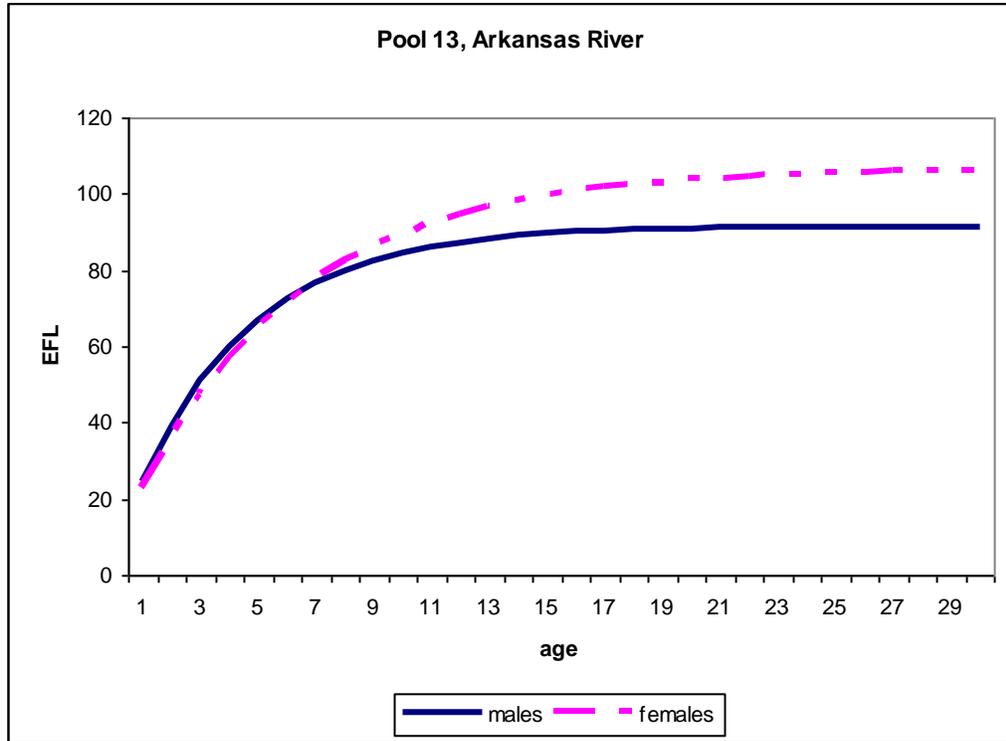
Figure 2.5.24. Growth curves for male and female Paddlefish of Pool 13 Arkansas River basin, Arkansas. Growth parameters from Leone et al., 2011.
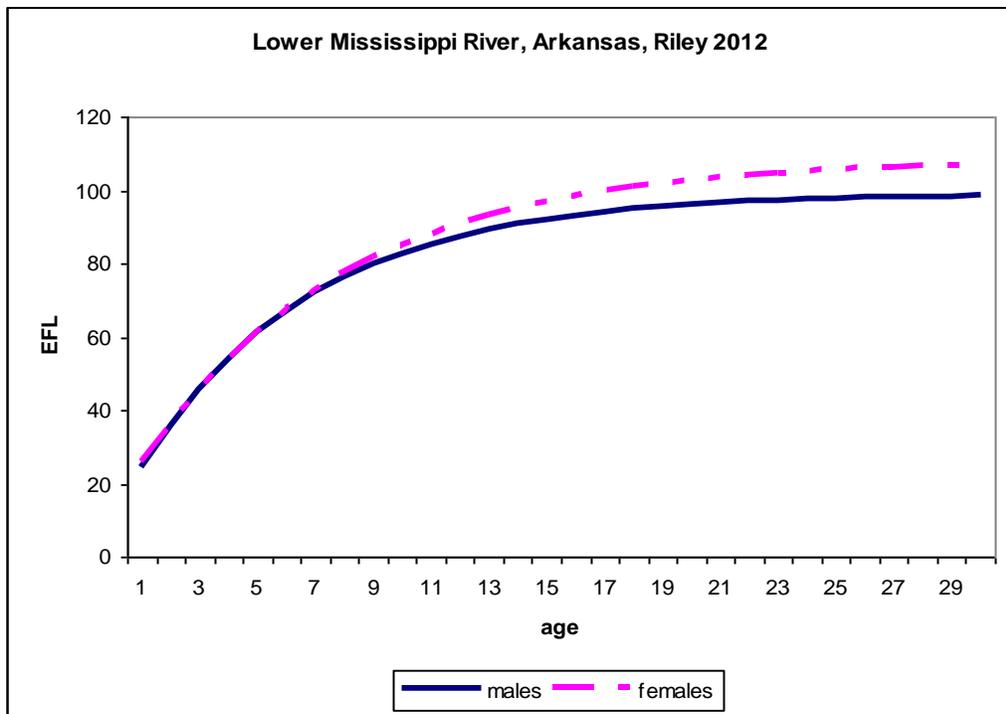
Figure 2.5.25. Growth curves for male and female Paddlefish of Lower Mississippi River, Arkansas. Growth parameters from Risely et al., 2012.
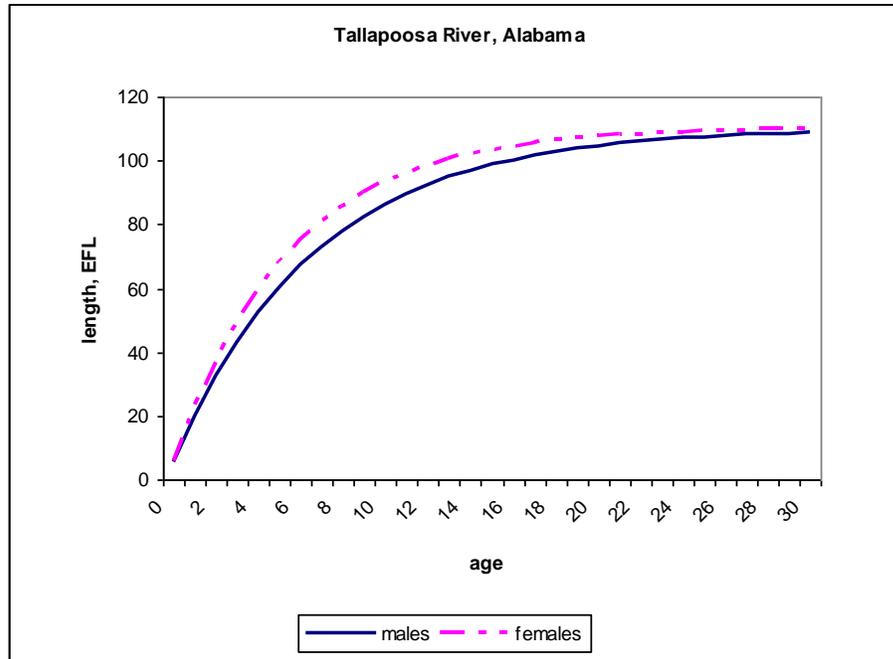
Figure 2.5.26. Growth curves for male and female Paddlefish of Tallapoosa River, Alabama. Growth parameters from Lein and Devries, 1998.
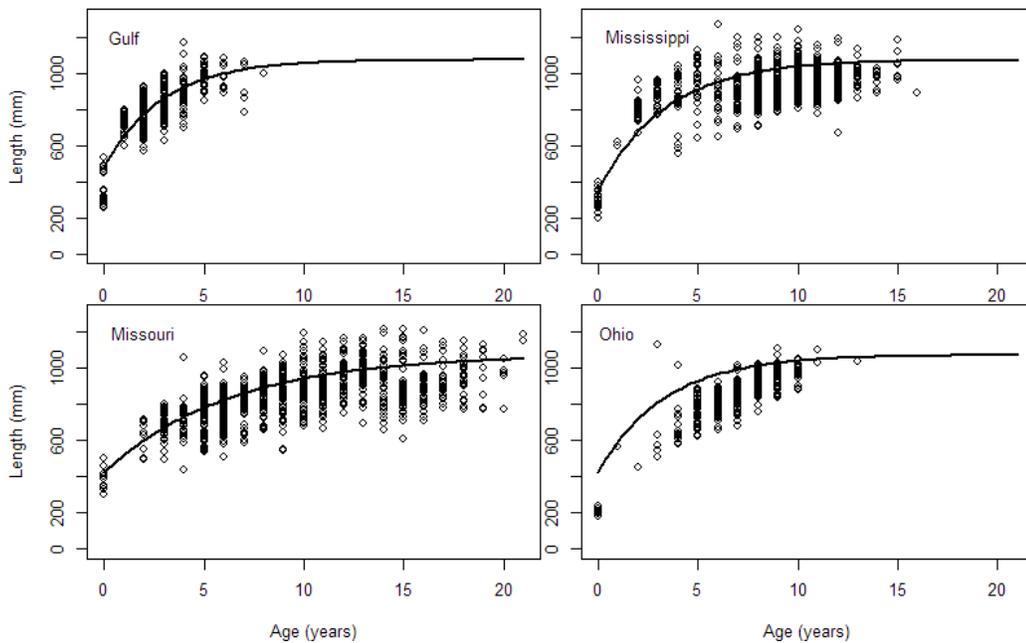
Figure 2.5.27. Estimated basin-wide mean von Bertalanffy growth curves (lines) and observed length at age (points) for Paddlefish (sexes combined). The fit appears to be worse for the Ohio basin, but most of the points are from Kentucky Lake, which has a substantially different growth pattern than the other two reaches in that basin.

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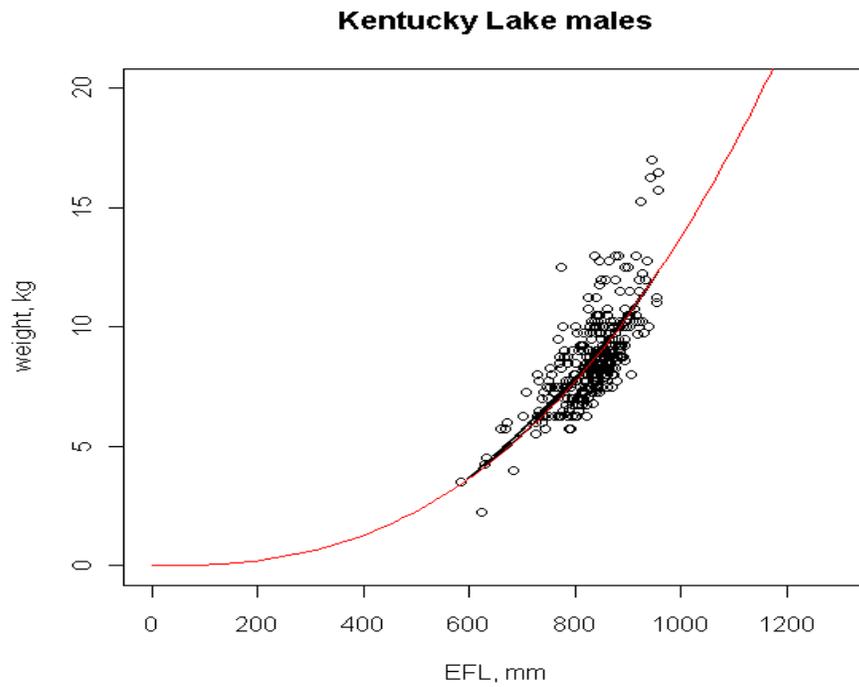
Figure 2.6.1. Length weight relationship for Kentucky lake males, data from Scholten and Bettoli, 2005.
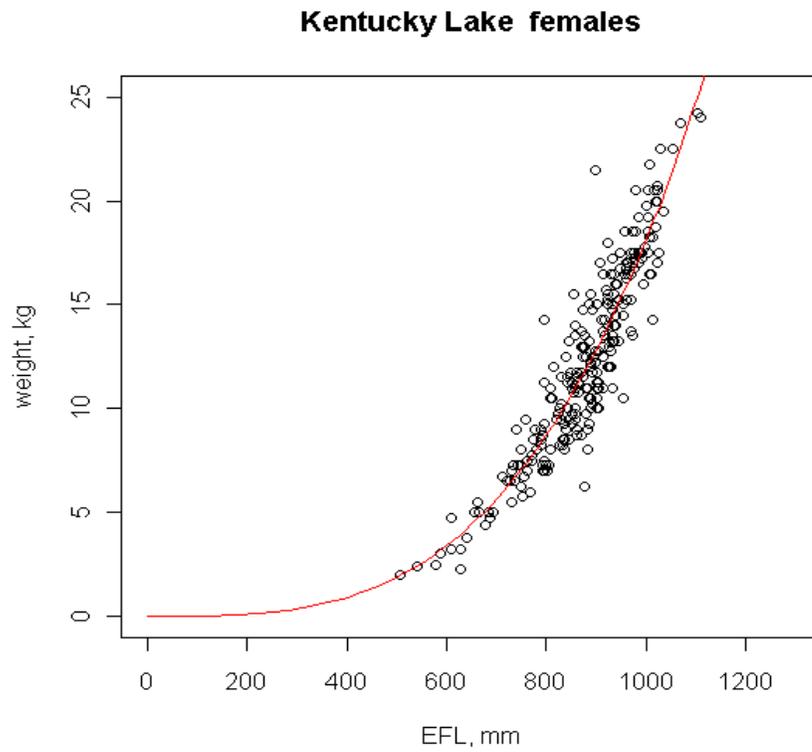
Figure 2.6.2. Length weight relationship for Kentucky lake females, data from Scholten and Bettoli, 2005.

Lower Mississippi females
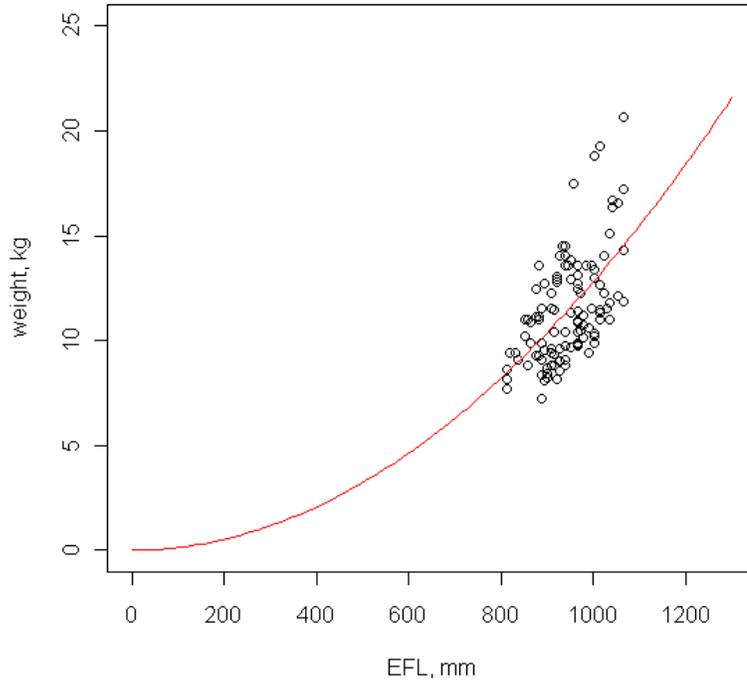
Figure 2.6.3. Lower Mississippi River female length weight relationship, data from Tripp et al., 2012.

Lower Mississippi males
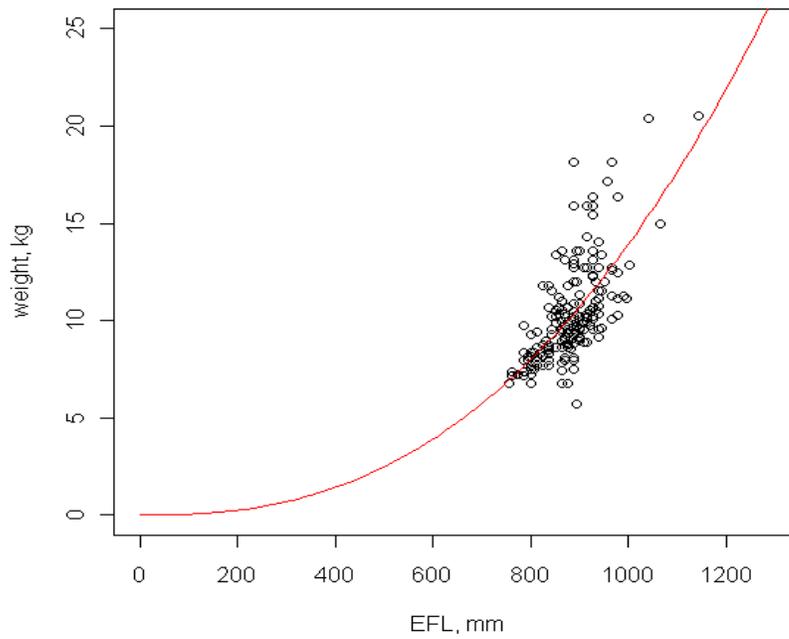
Figure 2.6.4. Lower Mississippi River male length weight relationship, data from Tripp et al., 2012.
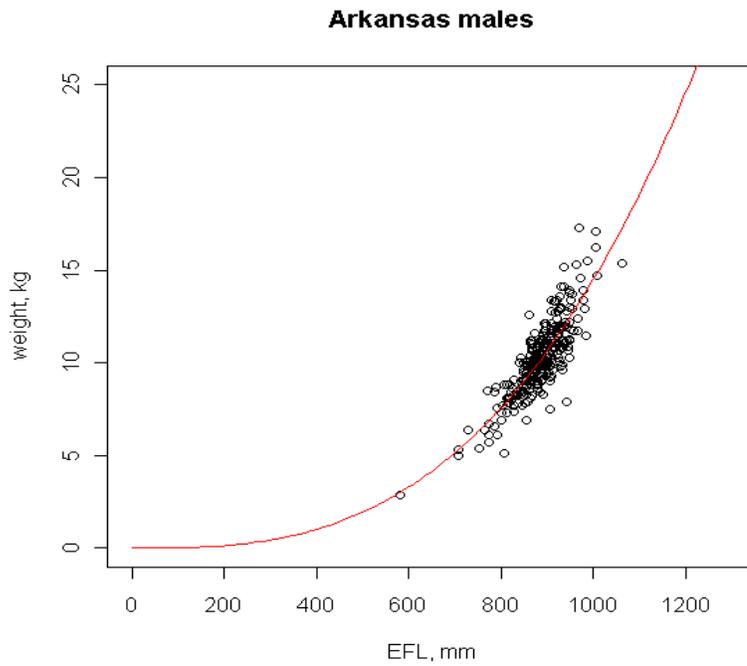
Figure 2.6.5. Length - weight relationship for Arkansas River Paddlefish (pools combined), data from Leone et al., 2011.
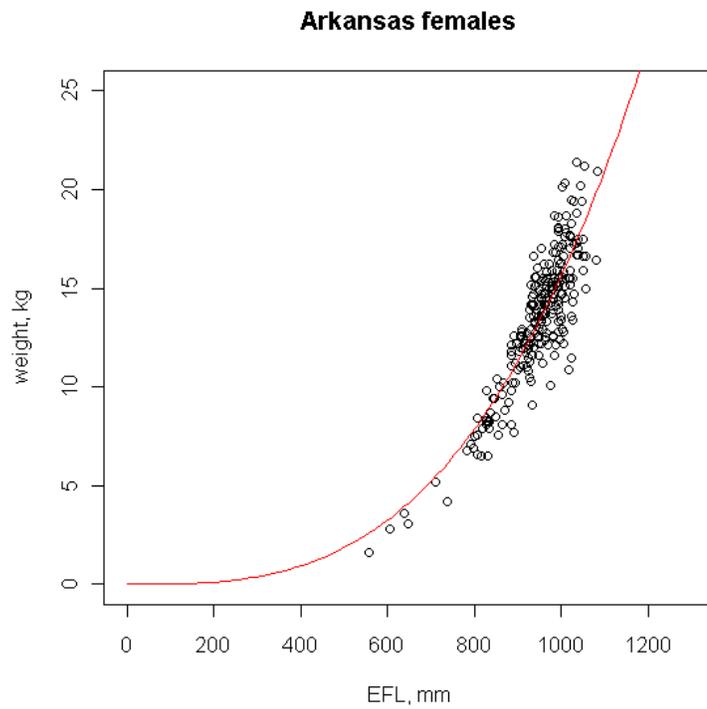
Figure 2.6.6. Length - weight relationship for Arkansas River female Paddlefish (pools combined), data from Leone et al., 2011.
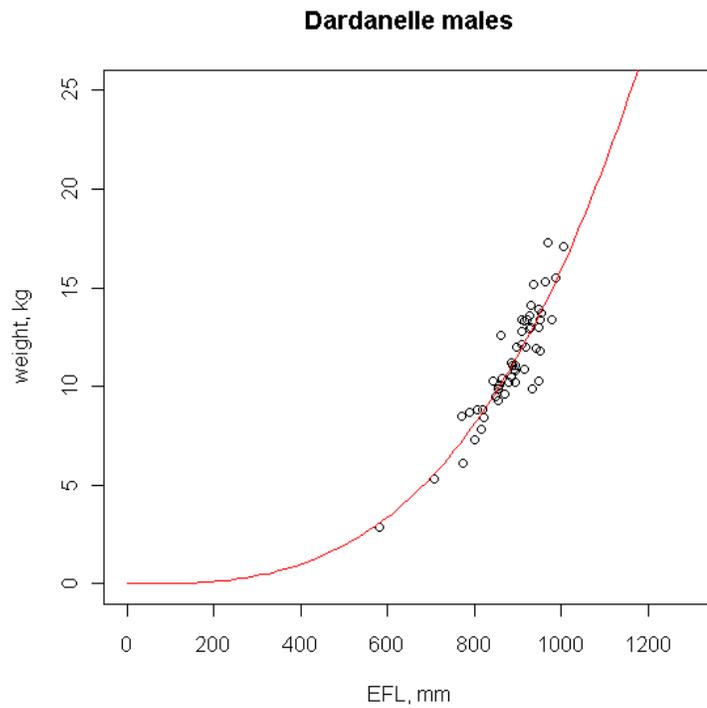
Figure 2.6.7. Length - weight relationship for Lake Dardanelle, Arkansas River male Paddlefish, data from Leone et al., 2011.
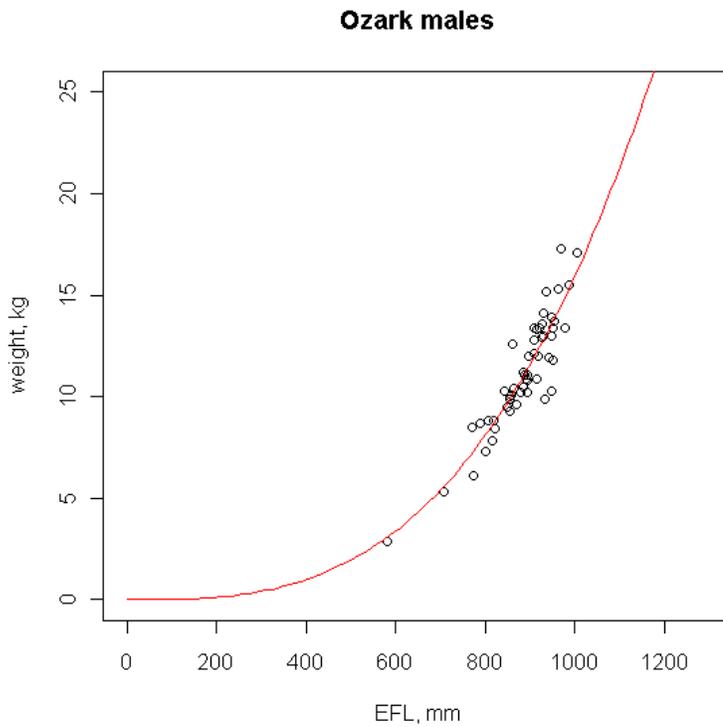
Figure 2.6.8. Length - weight relationship for Lake Ozark, Arkansas River male Paddlefish, data from Leone et al., 2011.

Missouri basin
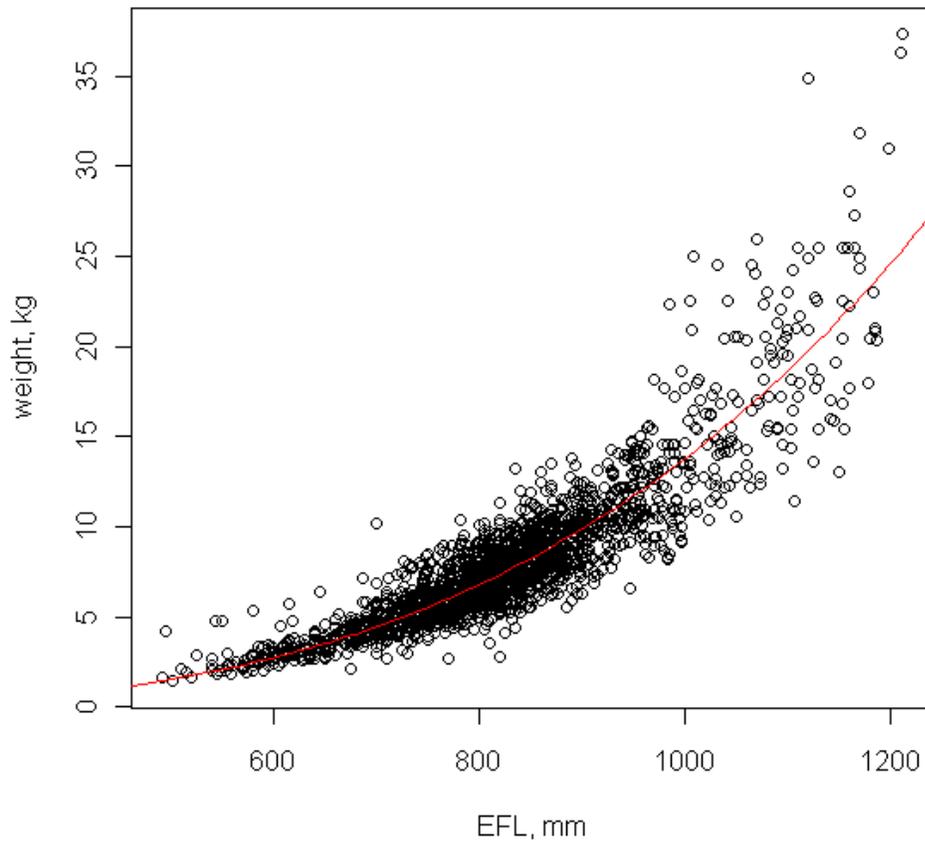
Figure 2.6.9. Length - weight relationship for Paddlefish (sexes combined) of the Missouri River basin, source: MICRA tagging database, 2012.

Mississippi basin
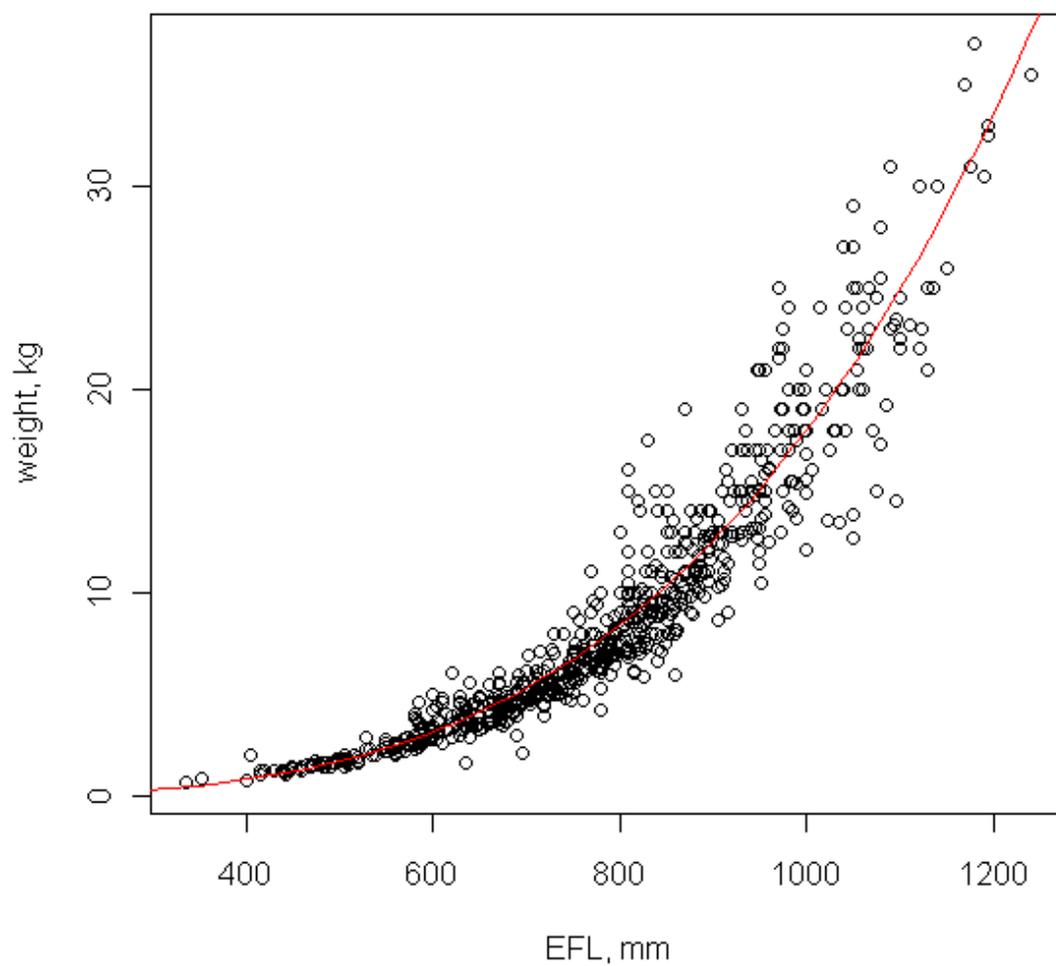
Figure 2.6.10. Length - weight relationship for Paddlefish (sexes combined) of the Mississippi River basin, source: MICRA tagging database, 2012.

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Figure 2.6.11. Length - weight relationship for female Paddlefish for Gulf of Mexico basin, source: MICRA tagging database, 2012.

Gulf basin, males
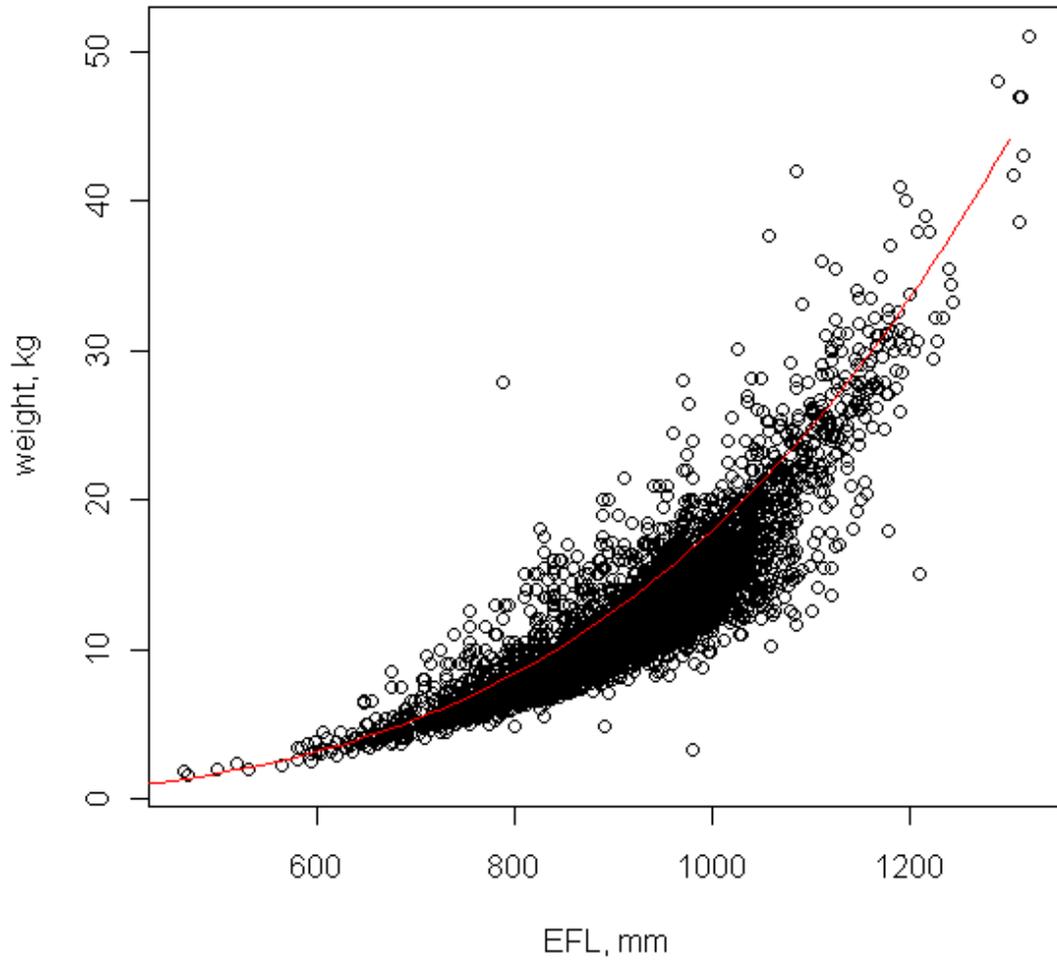
Figure 2.6.12. Length - weight relationship for male Paddlefish for Gulf of Mexico basin, source: MICRA tagging database, 2012.

Ohio basin, females
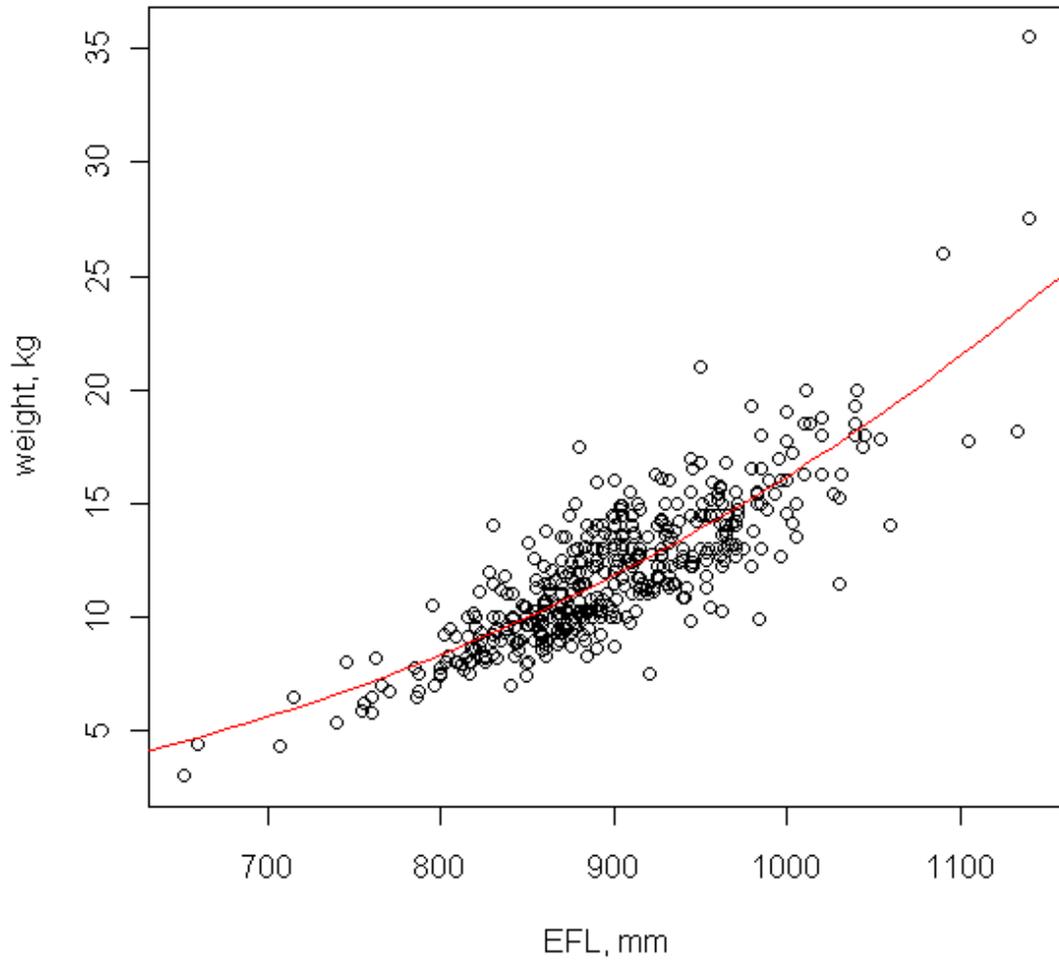
Figure 2.6.13. Length - weight relationship for female Paddlefish for Ohio River basin, source: MICRA tagging database, 2012.

Ohio basin, males
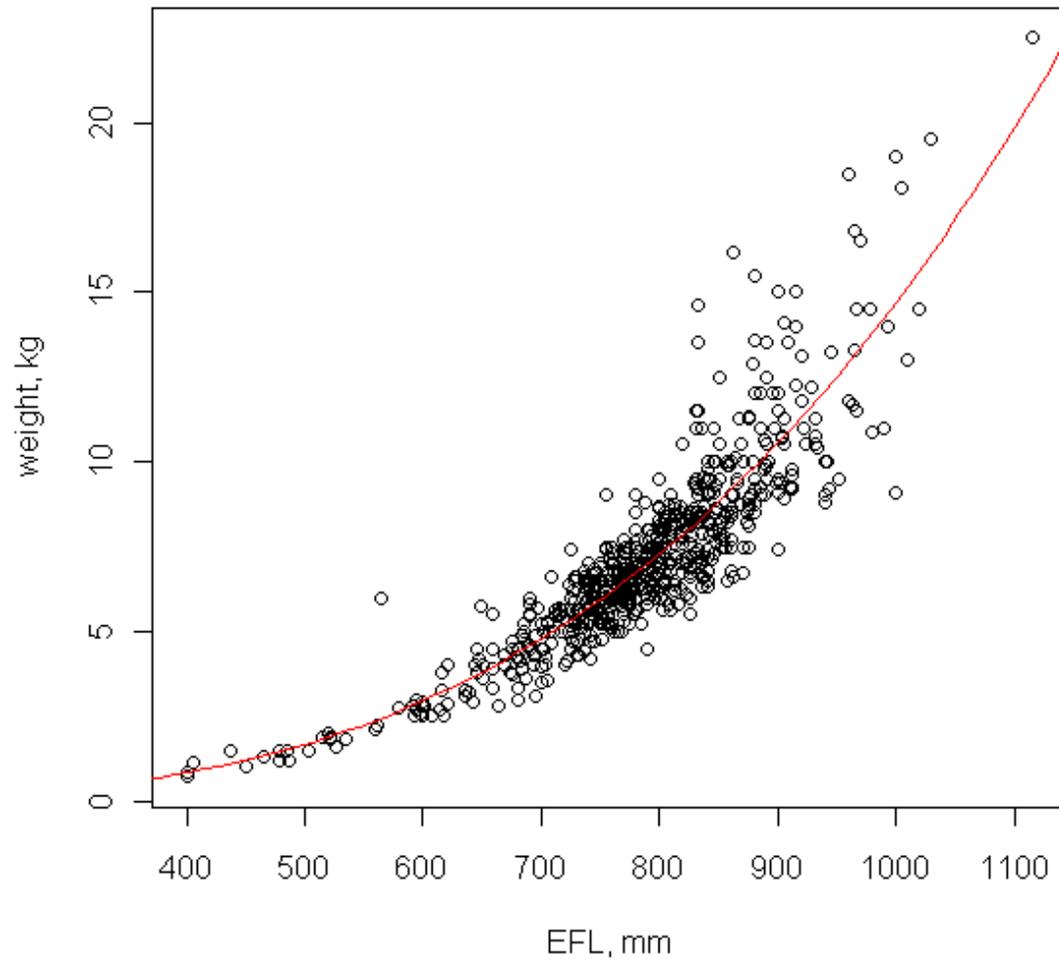
Figure 2.6.14. Length - weight relationship for male Paddlefish for Ohio River basin, source: MICRA tagging database, 2012.
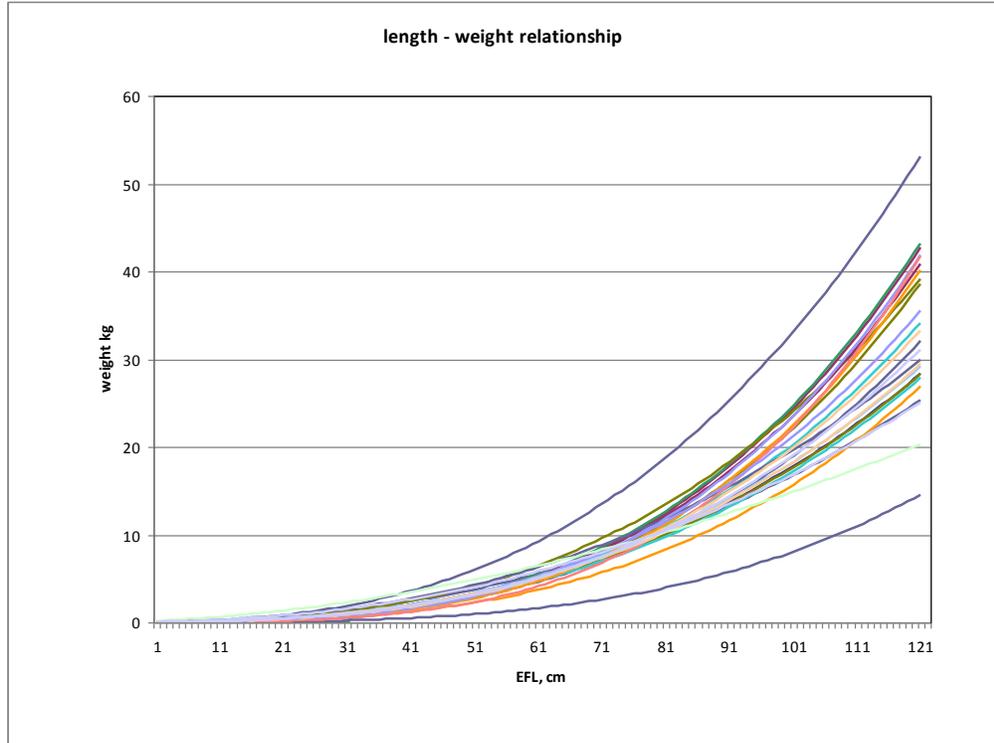
Figure 2.6.15. Length –weight curves plotted for all stocks with reported length weight parameters.
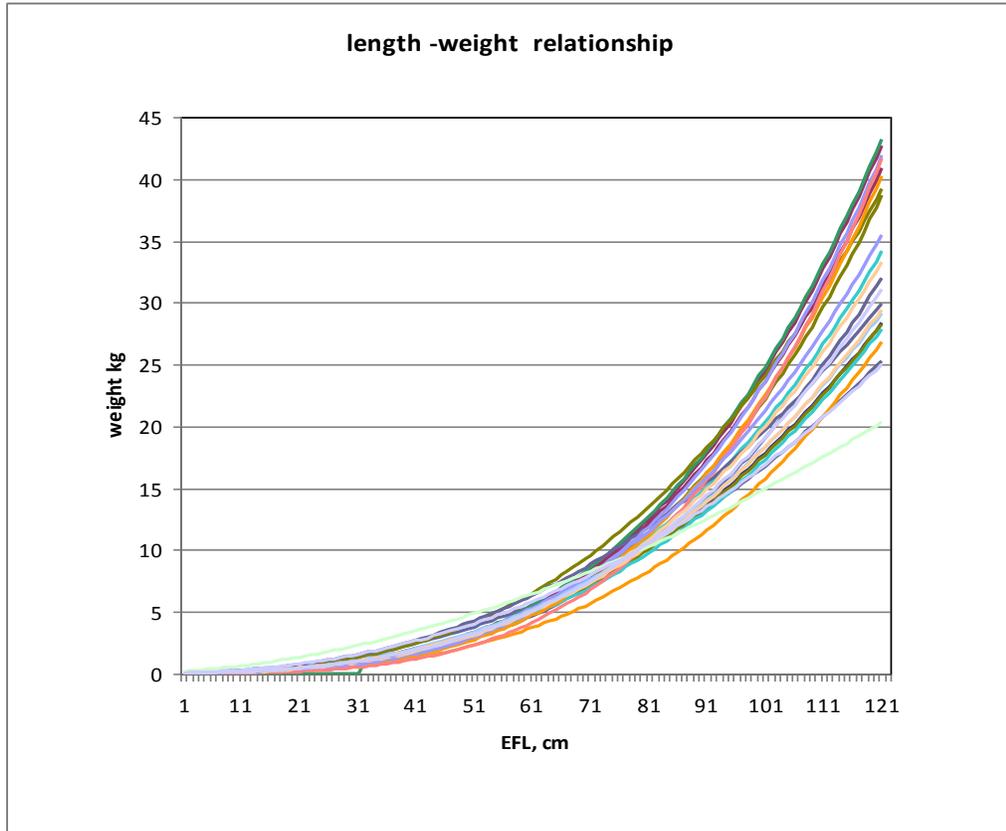
Figure 2.6.16. Length –weight curves plotted for all stocks with reported length weight parameters with data for Lake Barkley males and Kentucky Lake females (Bronte and Johnson, 1985) removed.
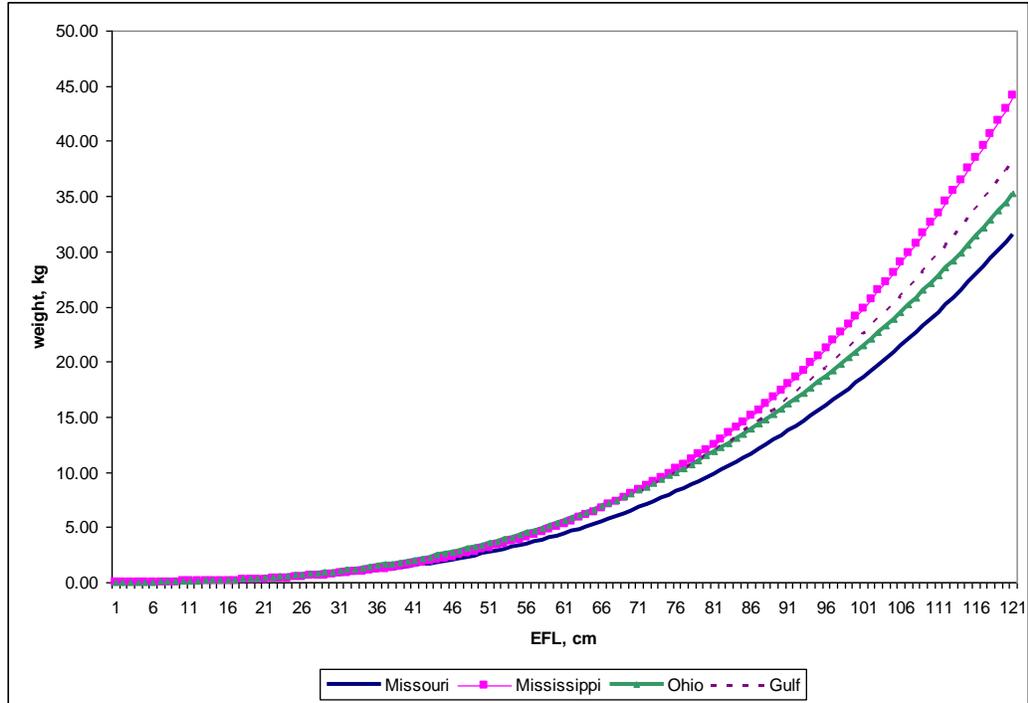
Figure 2.6.17. Length –weight curves plotted for Missouri, Mississippi, Ohio and Gulf basins.
Data source: MICRA tagging database, 2012.

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Arkansas River
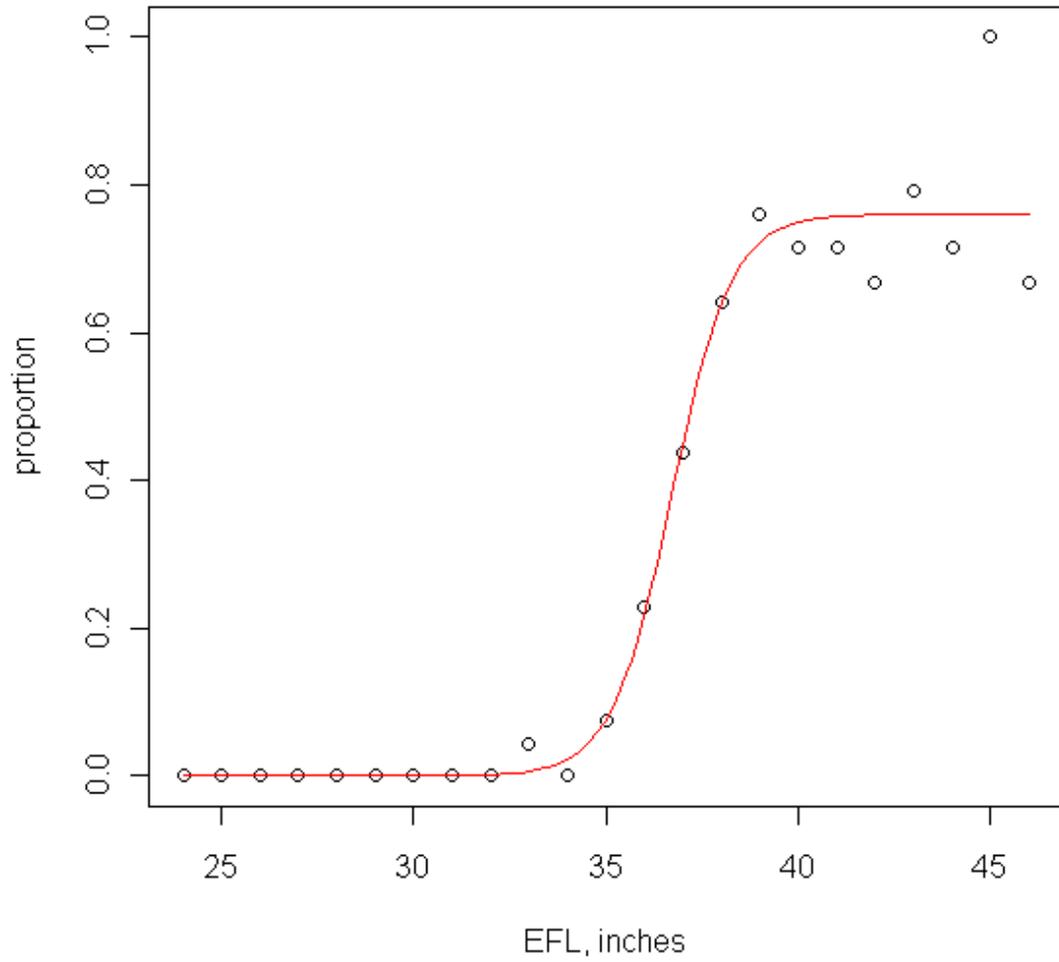
Figure. 2.7.1. Proportion gravid females as a function of size, Arkansas River, pools combined (Lake Dardanelle, Ozark and Pool 13) data from Leone et al., 2011.
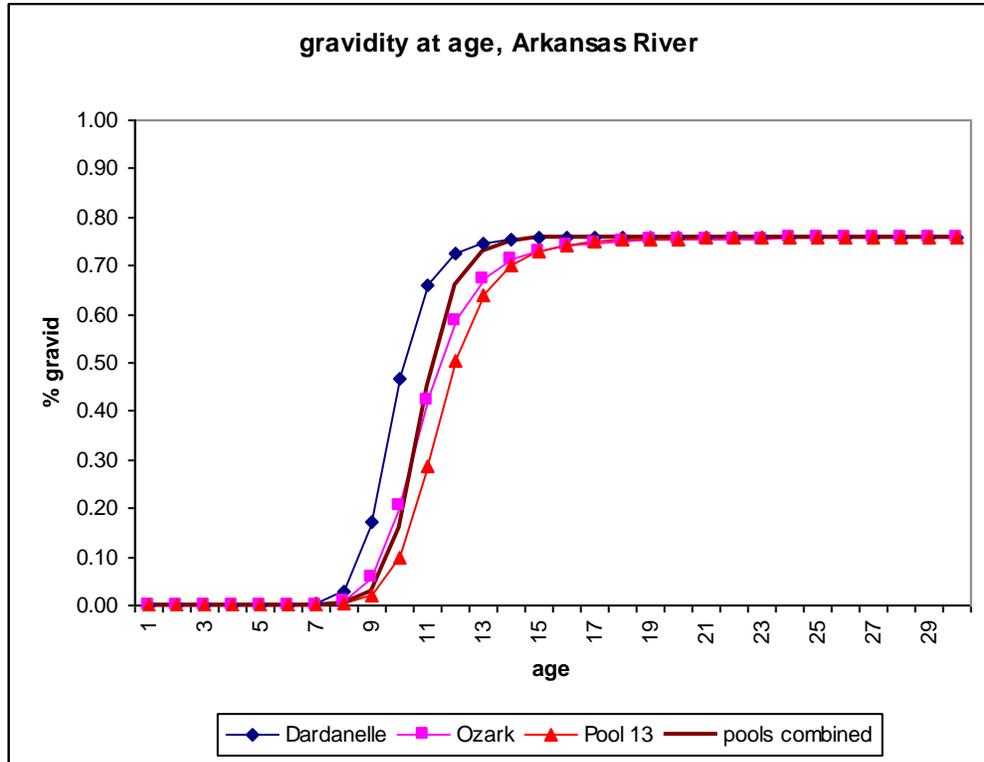
Figure. 2.7.2. Proportion gravid females at age, Arkansas River (Lake Dardanelle, Ozark Lake, Pool 13 and pools combined). data from Leone et al., 2011.

Kentucky Lake
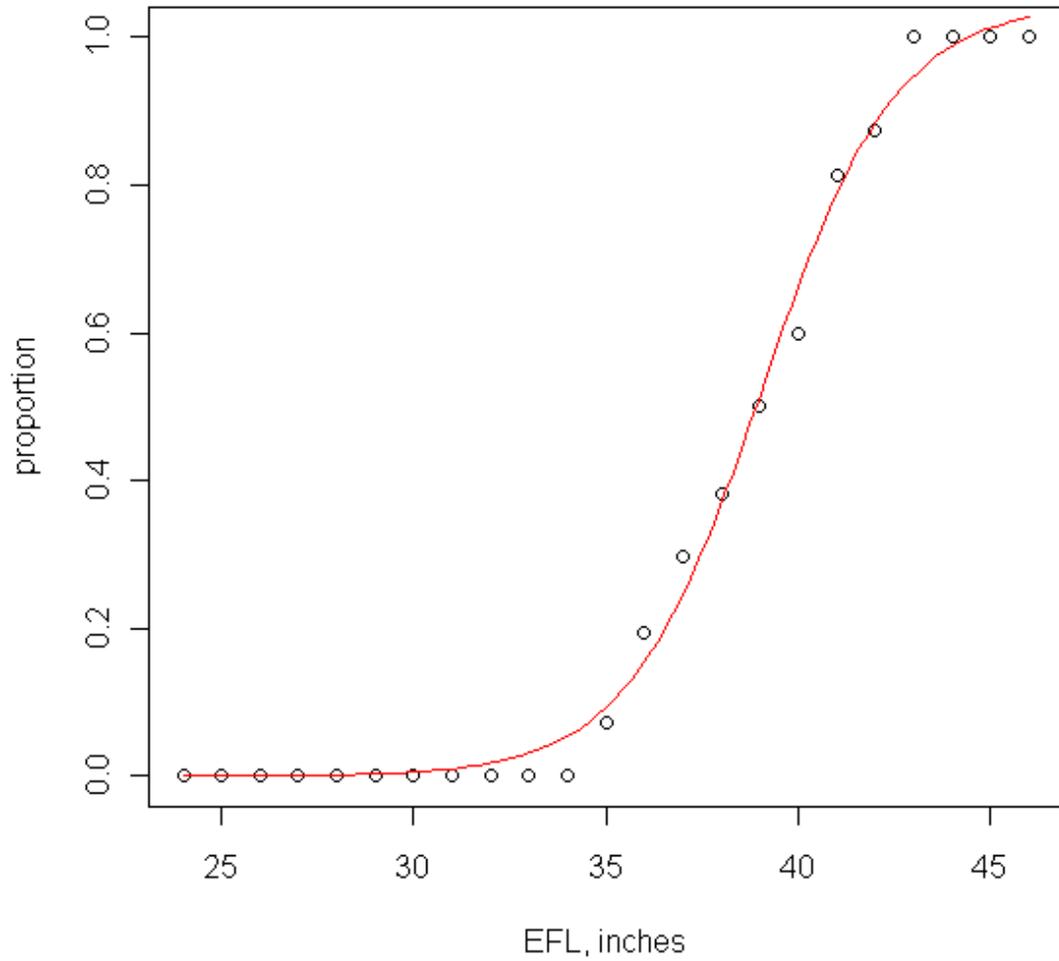
Figure 2.7.3. Proportion gravid females as a function of size, Kentucky Lake, data from Figure 5 of Scholten and Bettoli, 2005.
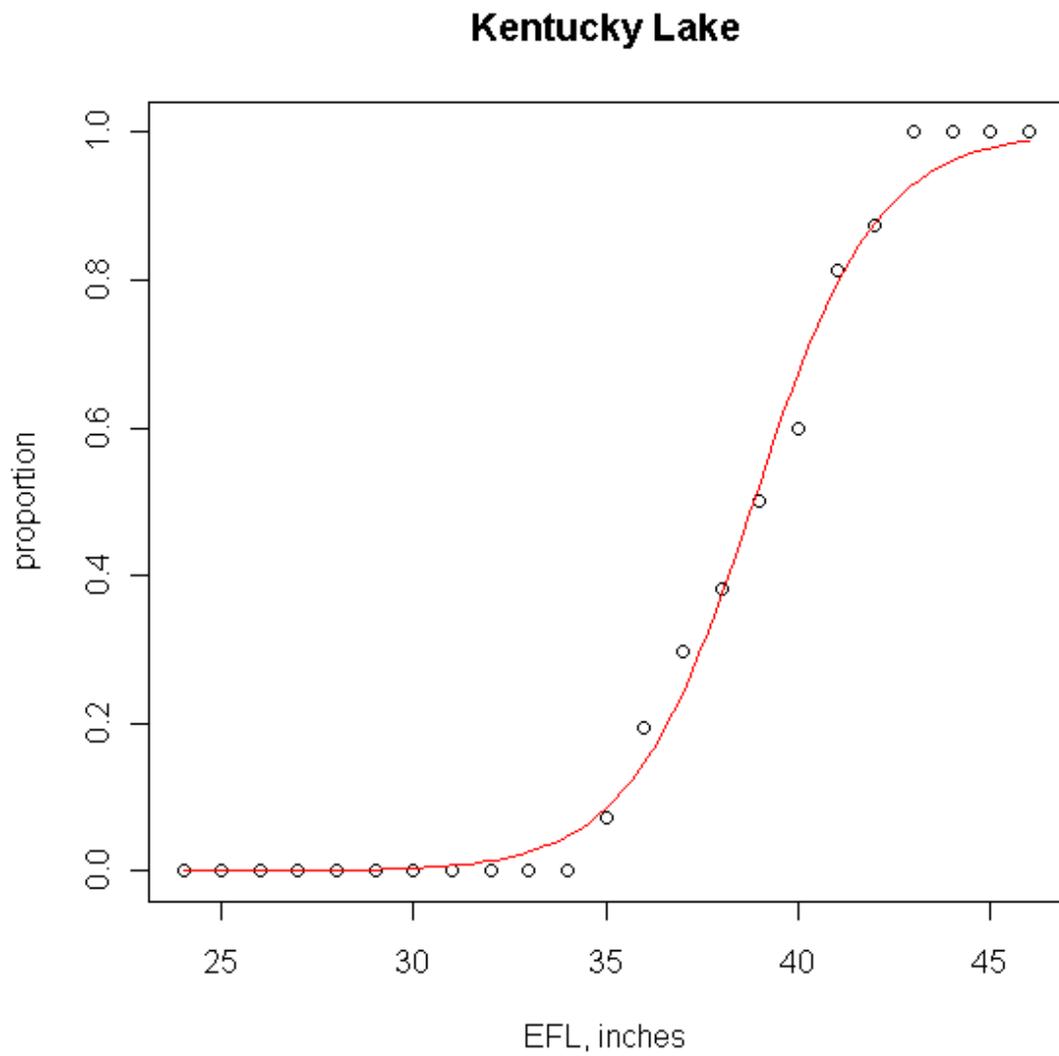
Kentucky Lake

Figure 2.7.4. Proportion gravid females as a function of size, Kentucky Lake. Data from Figure 5 of Scholten and Bettoli, 2005. The curve fit with asymptotic maturity m fixed at m = 1.
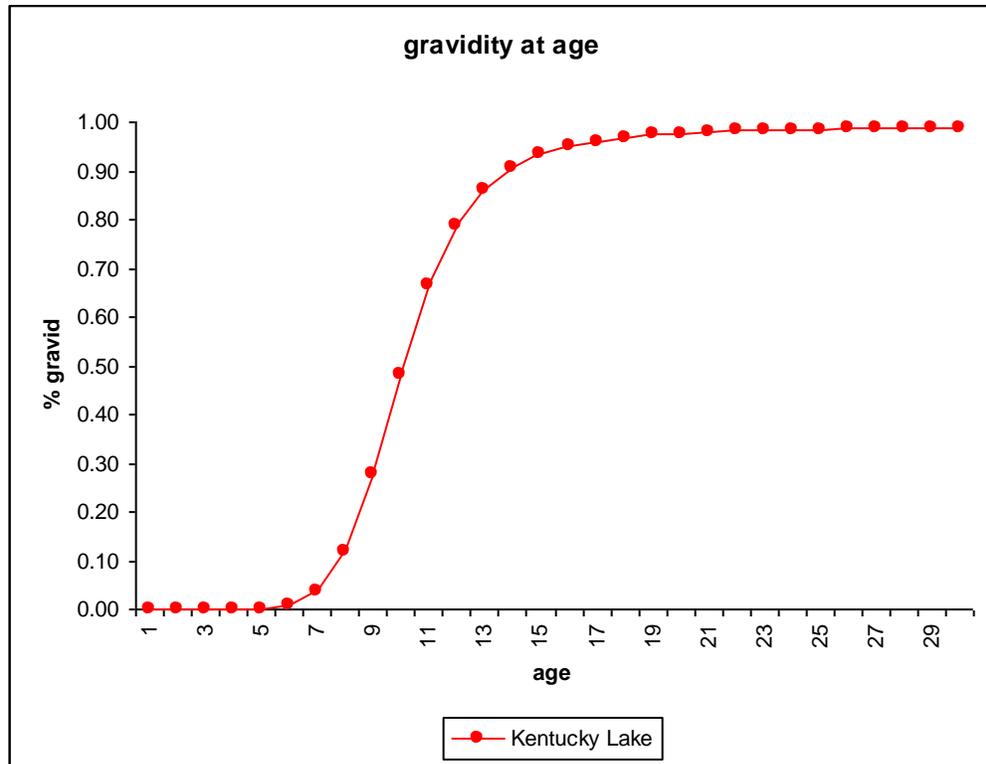
Figure 2.7.5. Proportion gravid females as a function of age, Kentucky Lake. Data from Figure 5 of Scholten and Bettoli, 2005.
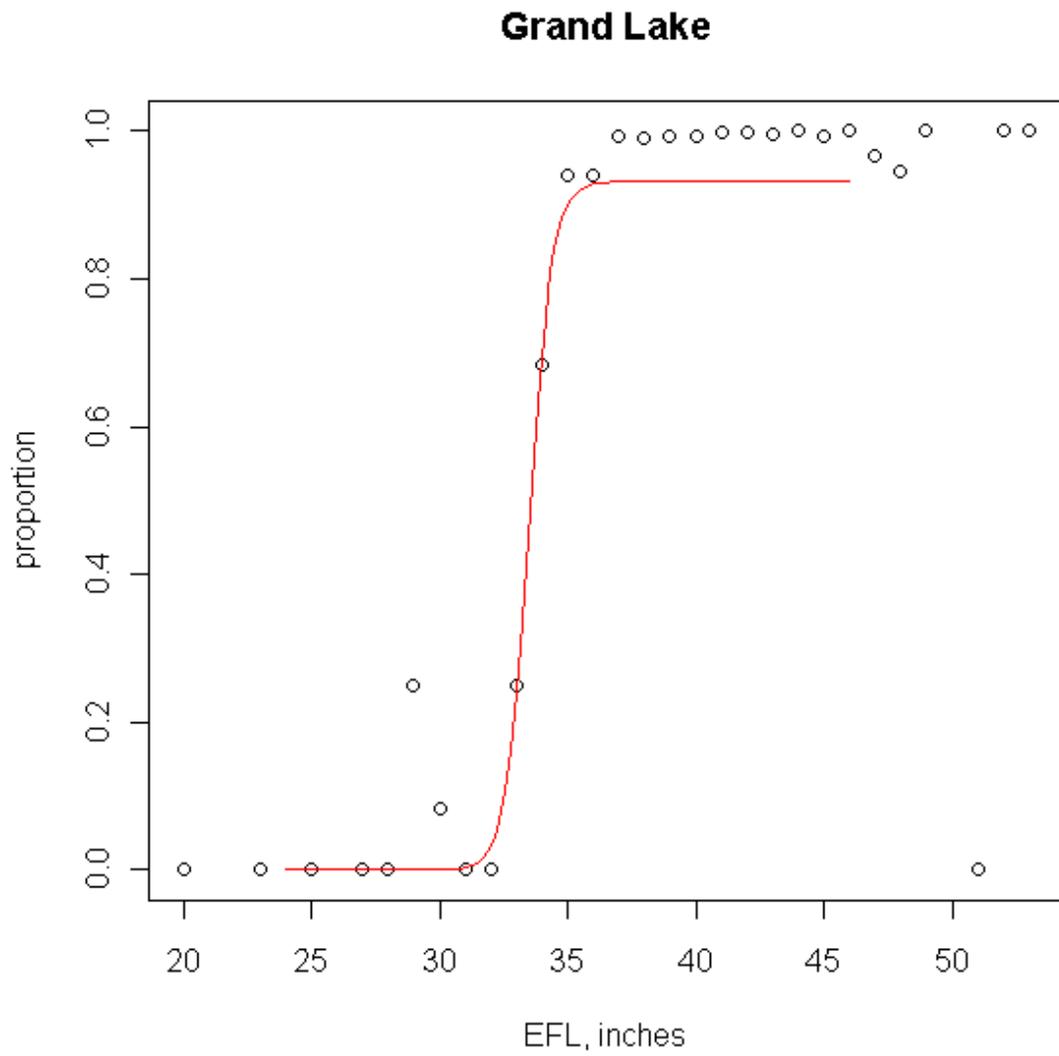
Figure 2.7.6. Proportion gravid females as a function of size, Grand Lake. Data provided by Oklahoma Department of Wildlife Conservation.
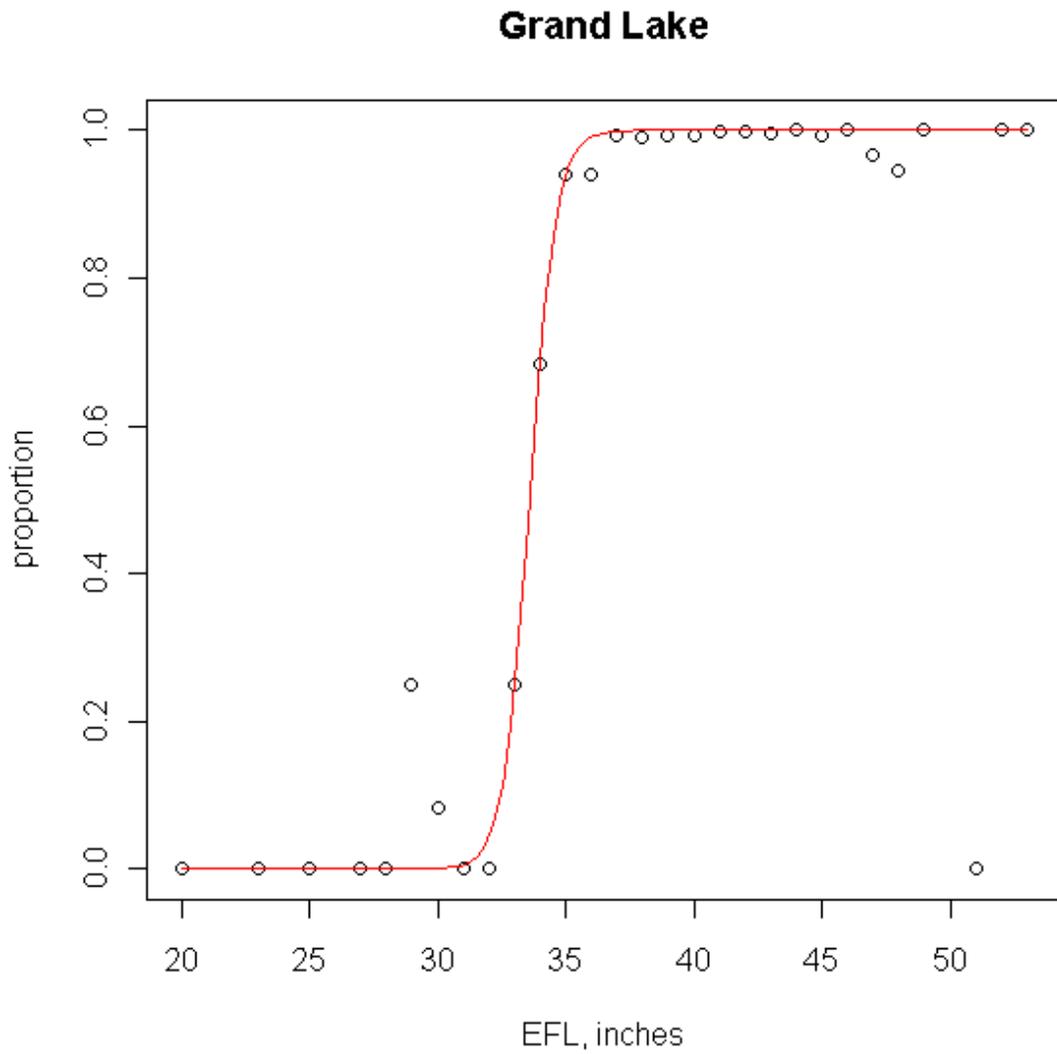
Grand Lake

Figure 2.7.7. Proportion gravid females as a function of size, Grand Lake. The curve fit with asymptotic maturity m fixed at m = 1. Data provided by Oklahoma Department of Wildlife Conservation.
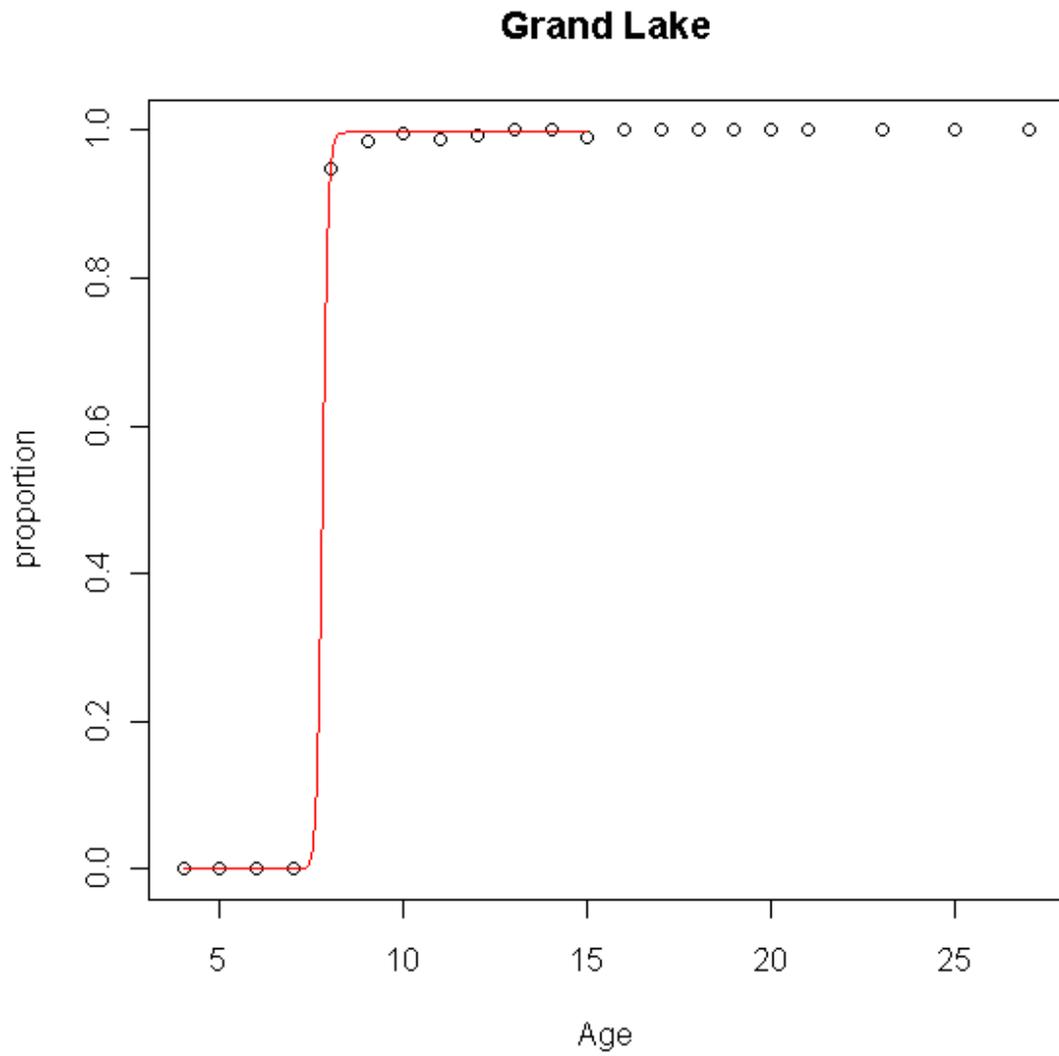
Figure 2.7.8. Proportion gravid females as a function of age, Grand Lake. Data provided by Oklahoma Department of Wildlife Conservation.
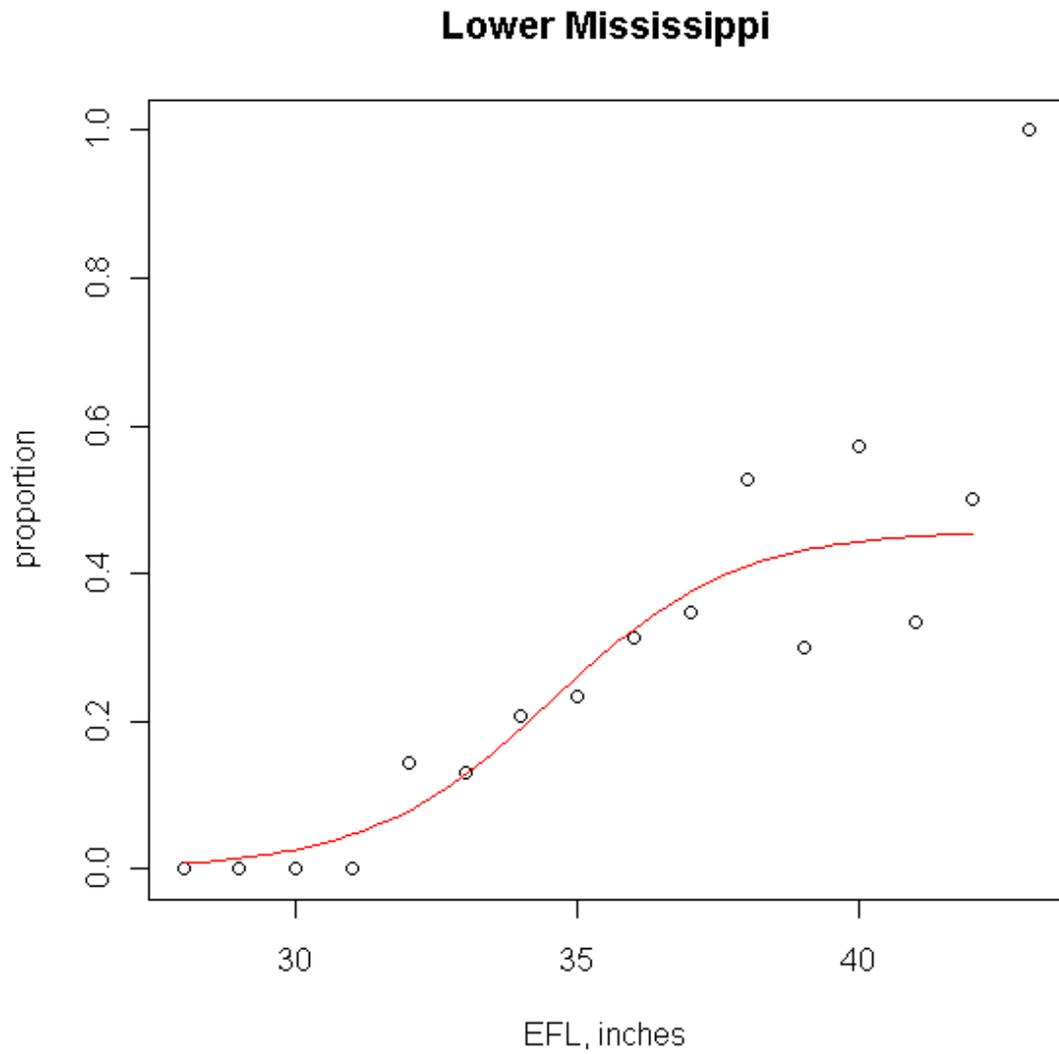
Figure 2.7.9. Proportion gravid females as a function of size, Lower Mississippi River, data from Risely,2012.

Lower Mississippi
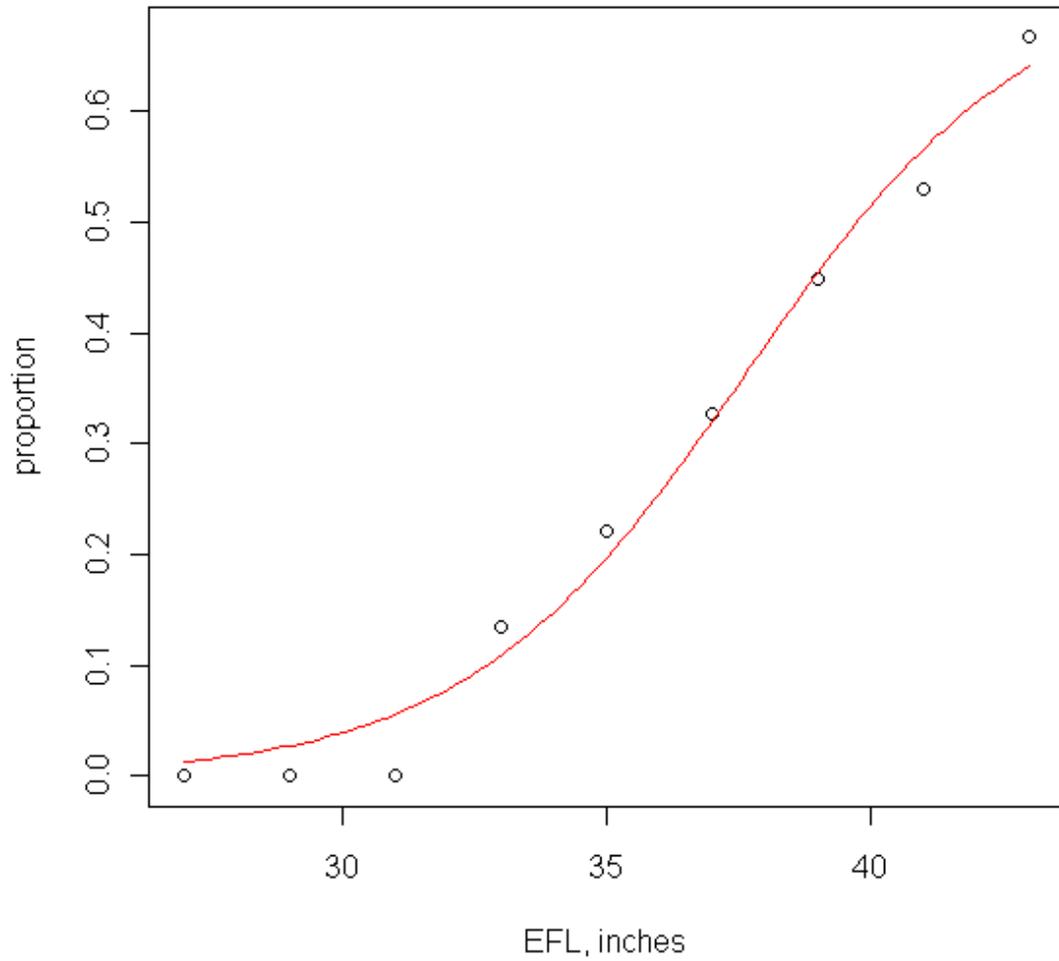
Figure 2.7.10. Proportion gravid females as a function of size, Lower Mississippi River, data from Risley, 2012.   The curve was fit with size intervals of two inches.
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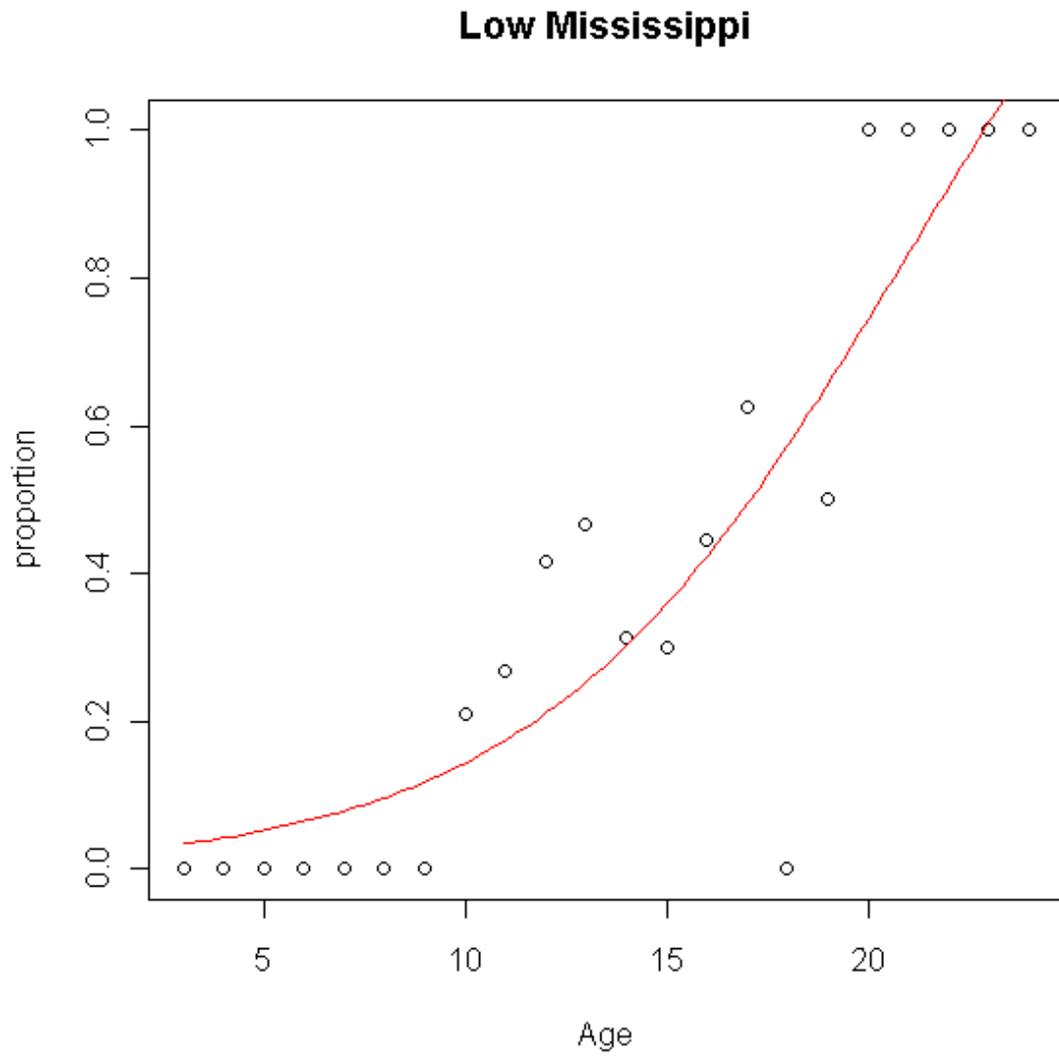
Figure 2.7.11. Proportion gravid females as a function of age, Lower Mississippi River, data from Risley (2012).
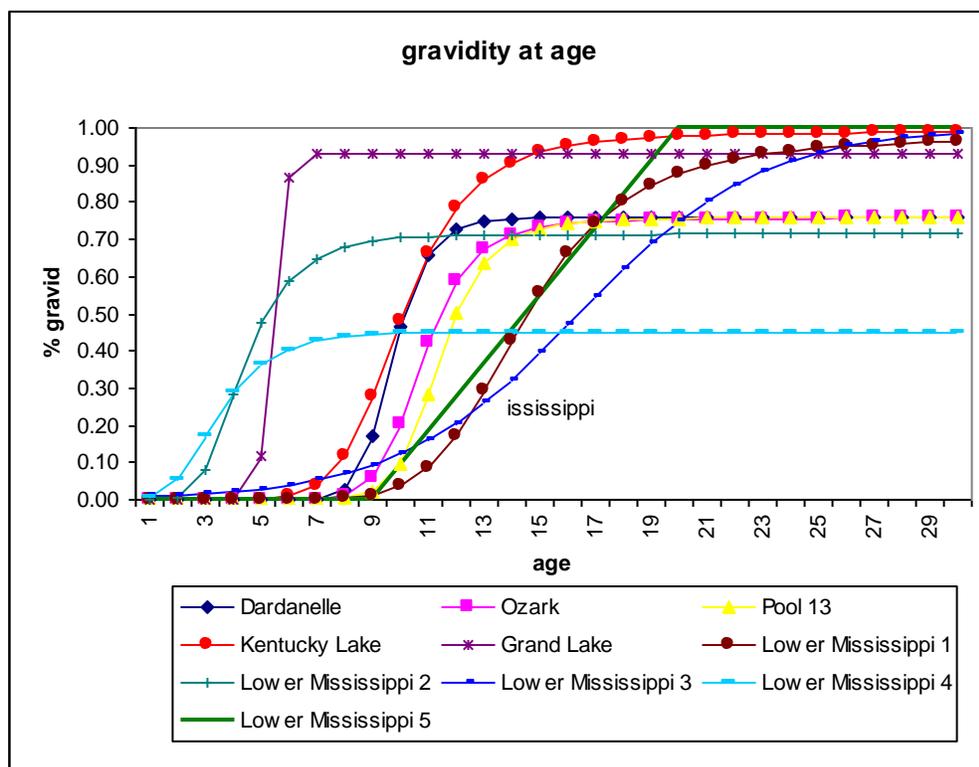
Figure 2.7.12. Proportion gravid females as a function of age estimated in this study for various populations. Curves for the Lower Mississippi reflect various calculations methods.
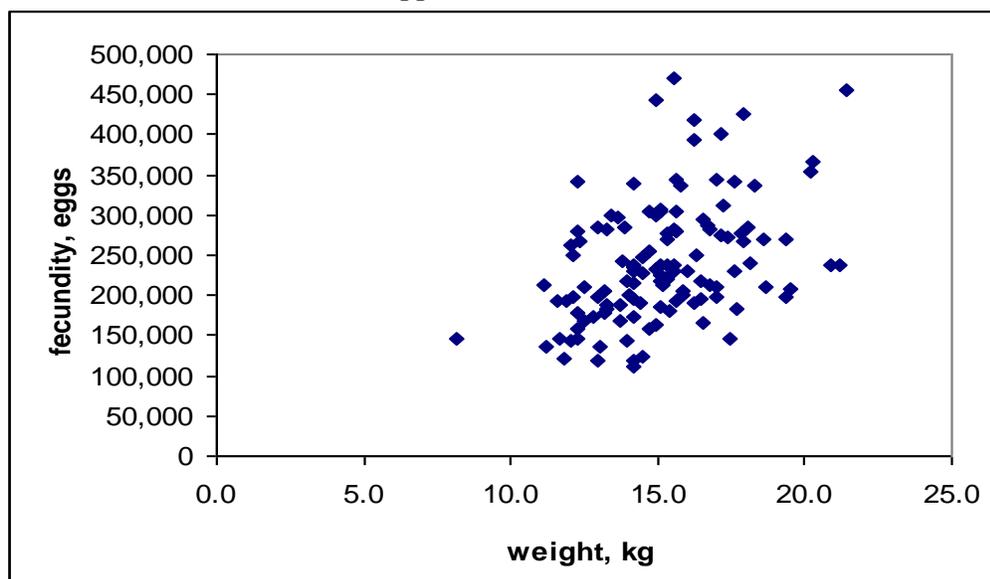
Figure 2.8.1. Fecundity (thousands of eggs) as a function of weight (kg) for Paddlefish females of Arkansas River (Lake Dardanelle, Lake Ozark and Pool 13). Data provided by Arkansas Game and Fish Commission and reported in Leone et al., 2011.
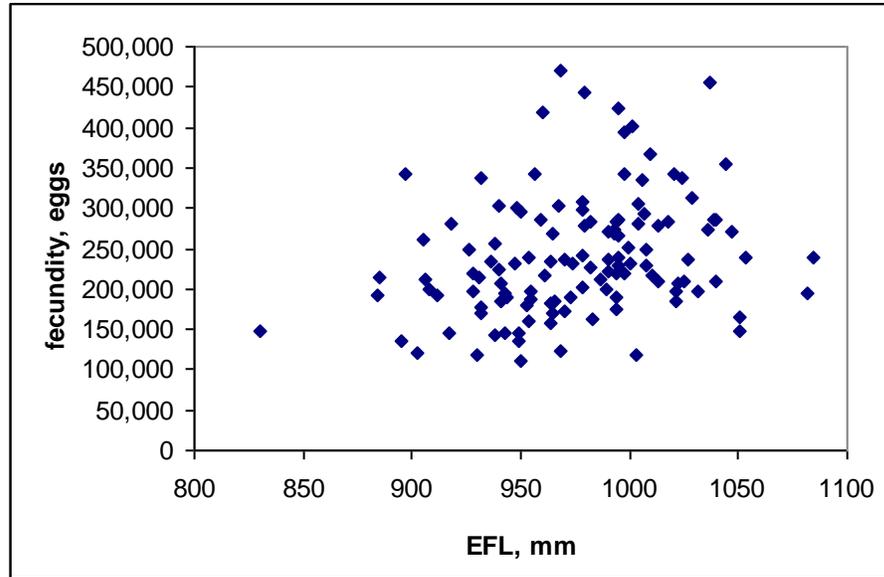
Figure 2.8.2. Fecundity (thousands of eggs) as a function of body length (EFL, mm) for Paddlefish females of Arkansas River (Lake Dardanelle, Lake Ozark and Pool 13). Data from Leone et al., 2012.
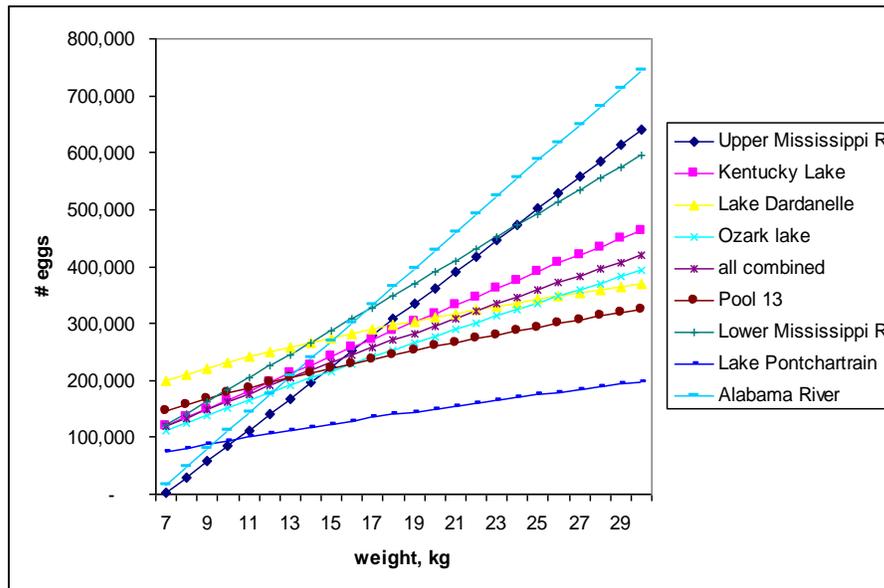
Figure 2.8.3. Fecundity (thousands of eggs) as a function of weight (kg) for various Paddlefish populations. Data sources presented in Table 2.8.2.
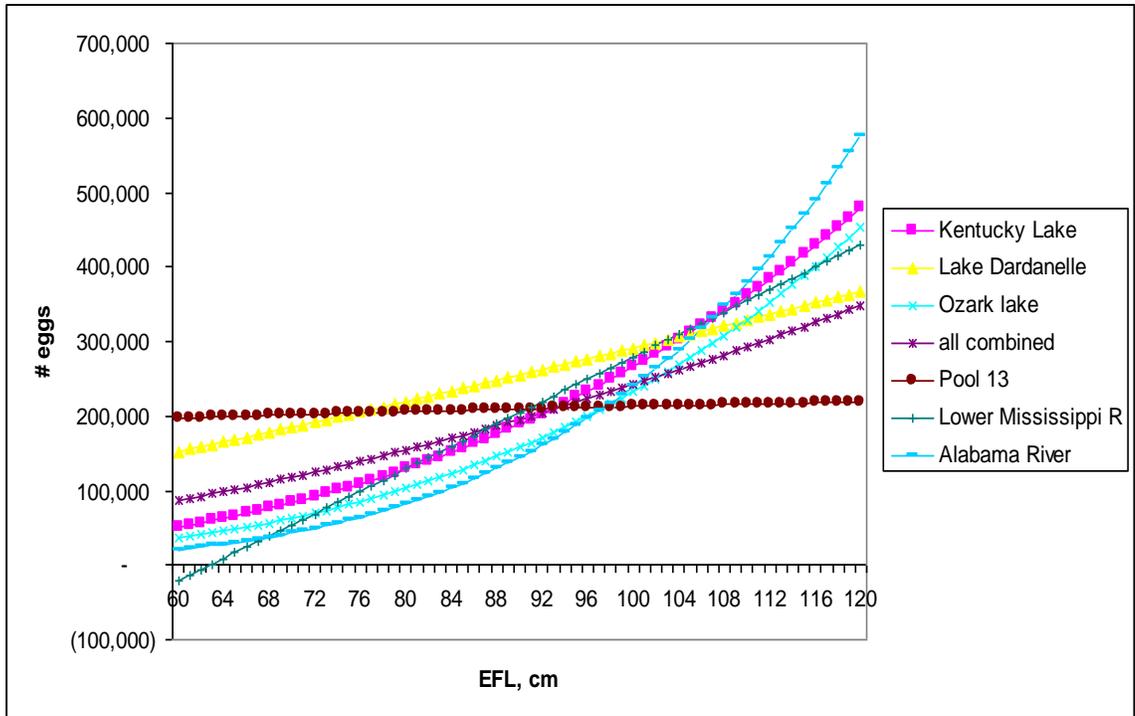
Figure 2.8.4. Fecundity (thousands of eggs) as a function of length (EFL) for various Paddlefish populations. Data sources presented in Table 2.8.2.
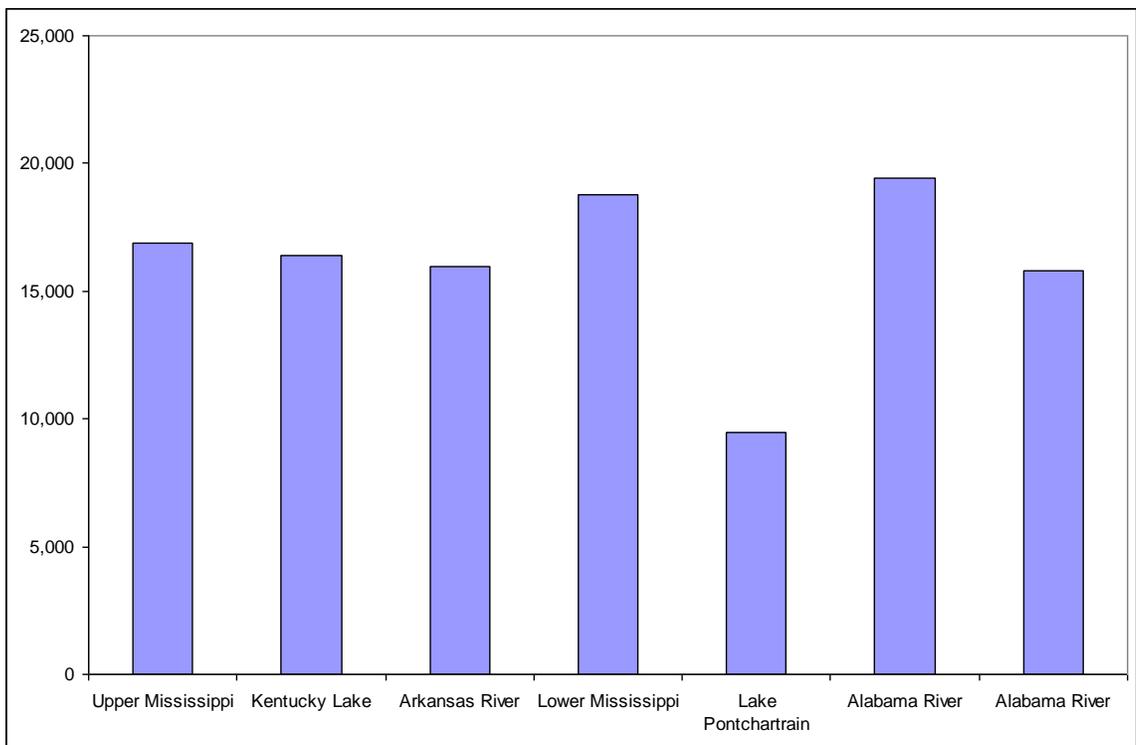
Figure 2.8.5. Average relative fecundity (thousands of eggs per kg body weight) for various Paddlefish populations. Data sources presented in Table 2.8.2.
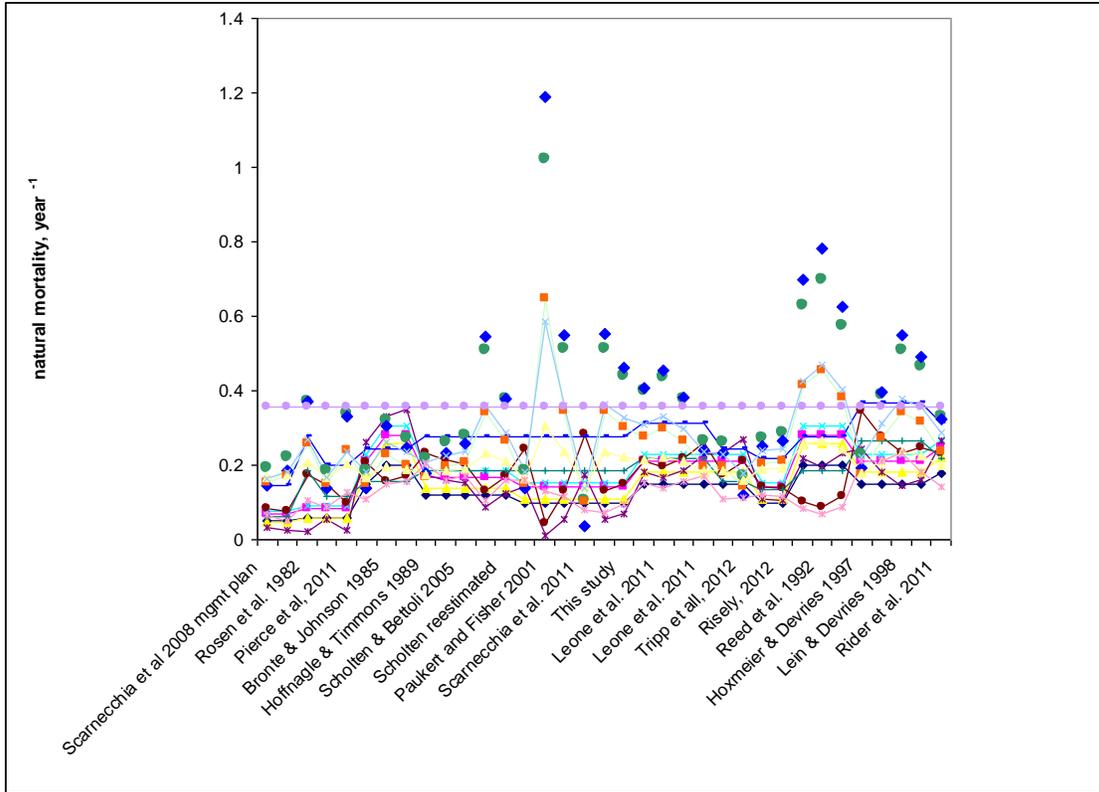
Figure 2.9.1. Natural mortality estimates (Y axis) based on various methods (X axis) calculated for Paddlefish stocks considered in this study.
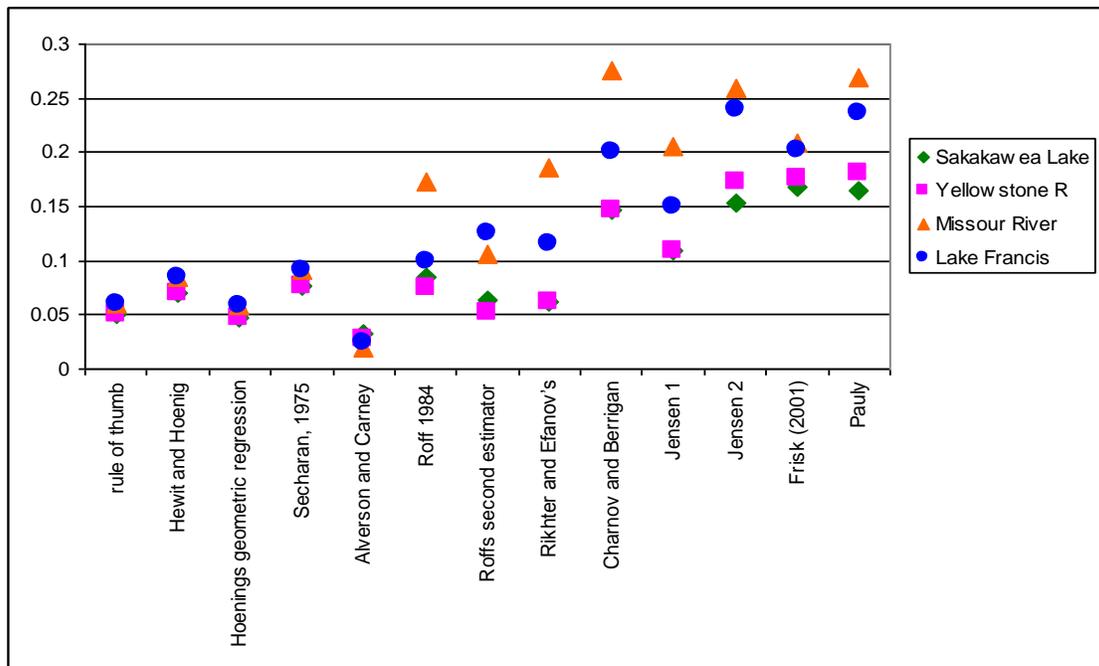
Figure 2.9.2. Natural mortality estimates (Y axis) based on various methods (X axis) calculated for Paddlefish of Sakakawea Lake, Yellowstone River, Lake Francis Case and the Missouri River.
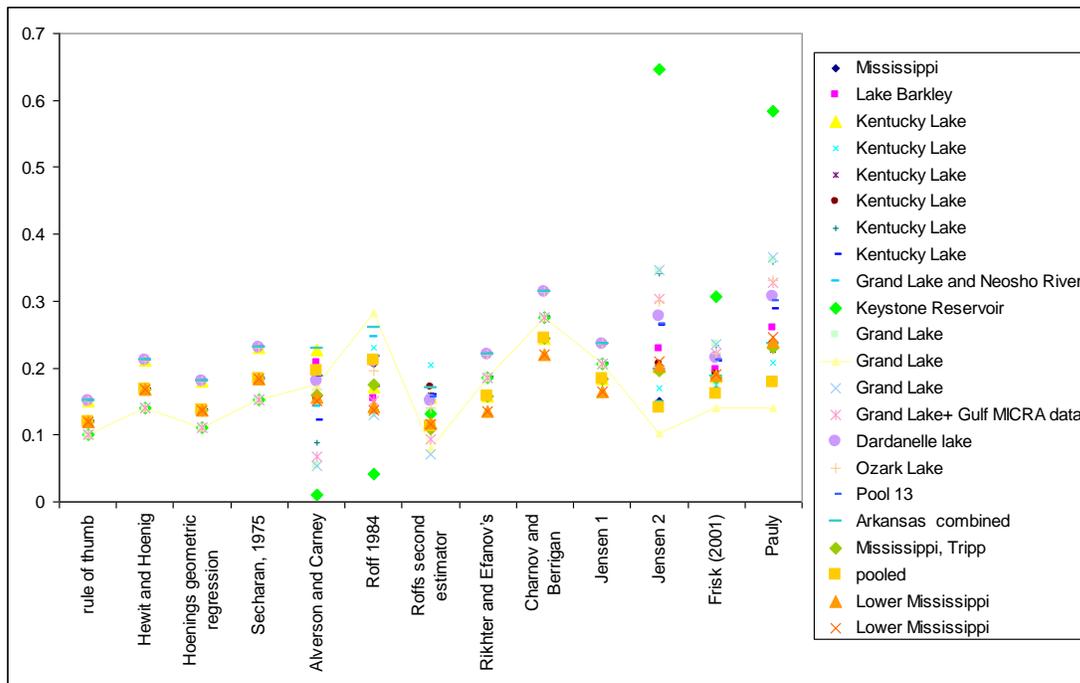
Figure 2.9.3. Natural mortality estimates (Y axis) based on various methods (X axis) calculated for Paddlefish of central region.
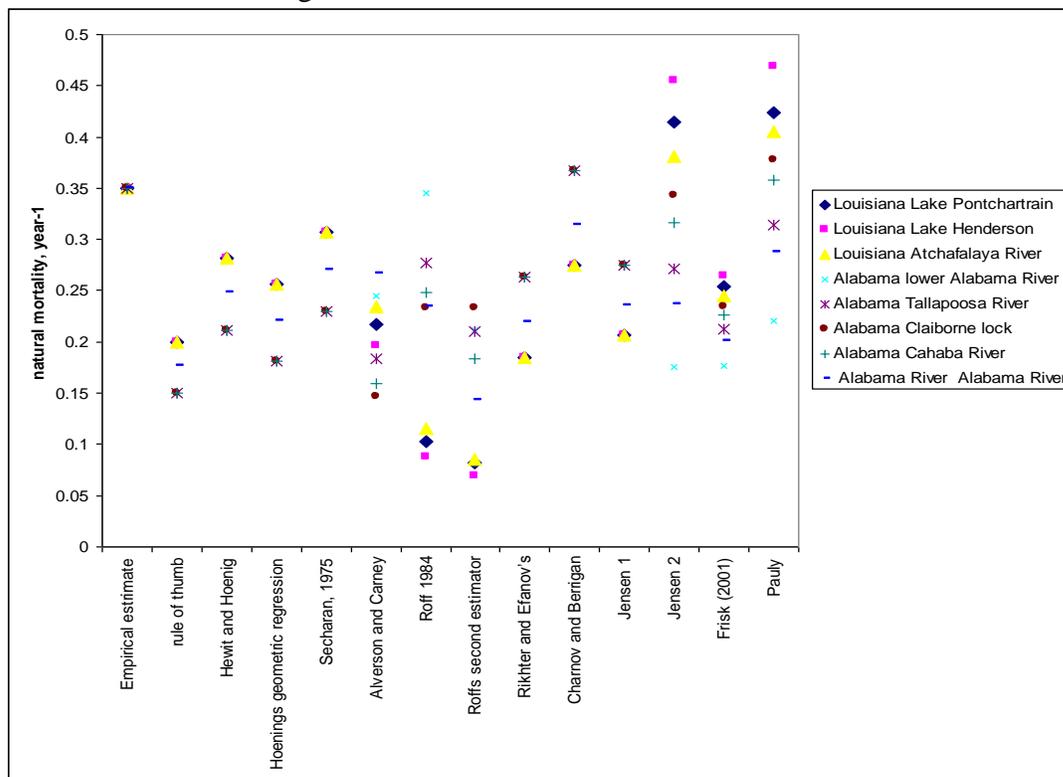
Figure 2.9.4. Natural mortality estimates (Y axis) based on various methods (X axis) calculated for Paddlefish of southern stocks.
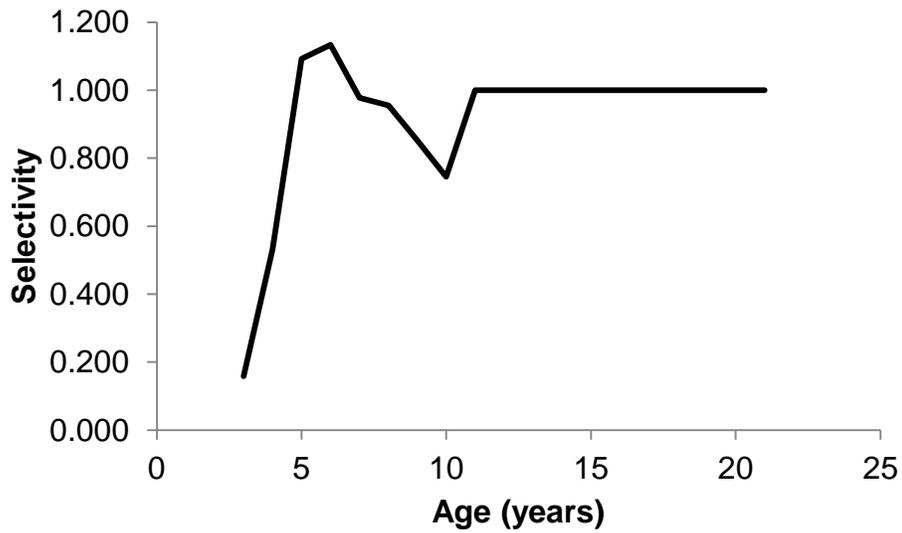
Figure 2.10.1. Estimated selectivity at age for Paddlefish in Lake Francis Case, South Dakota from the year class curves analysis.
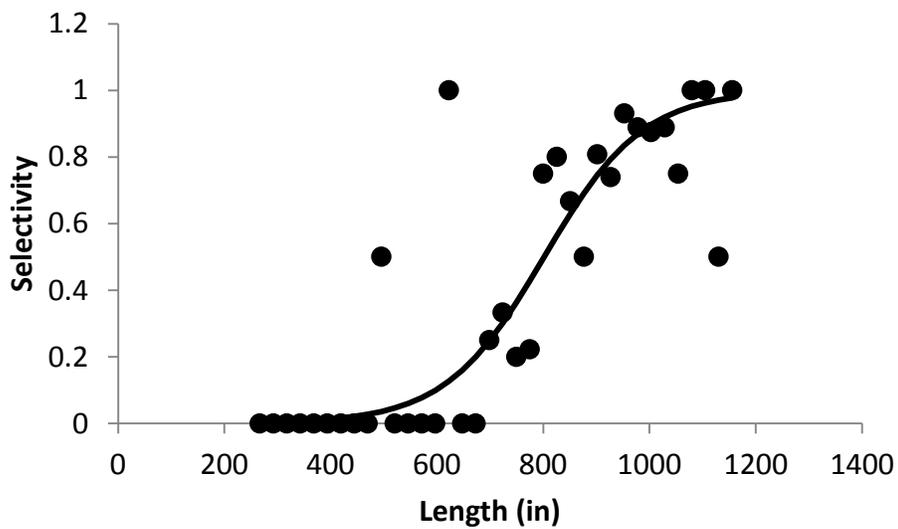
Figure 2.11.1. Estimated selectivity at length (line) and observed proportion at length in the catch (points) for gillnets from the gillnet-rotenone study of selectivity in Arkansas River.
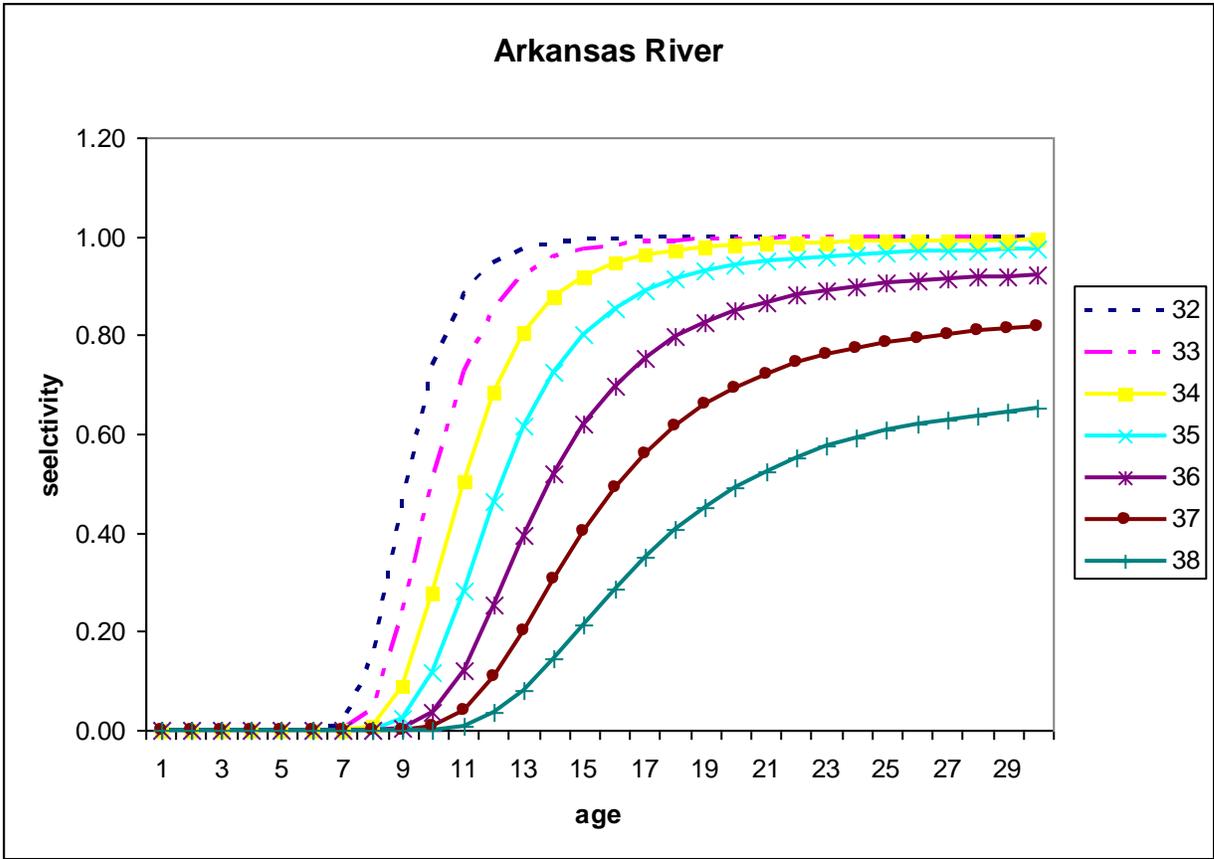
Figure 3.1.1. Partial recruitment (selectivity) for fishing mortality used in yield per recruit analysis for various levels of minimum legal size.
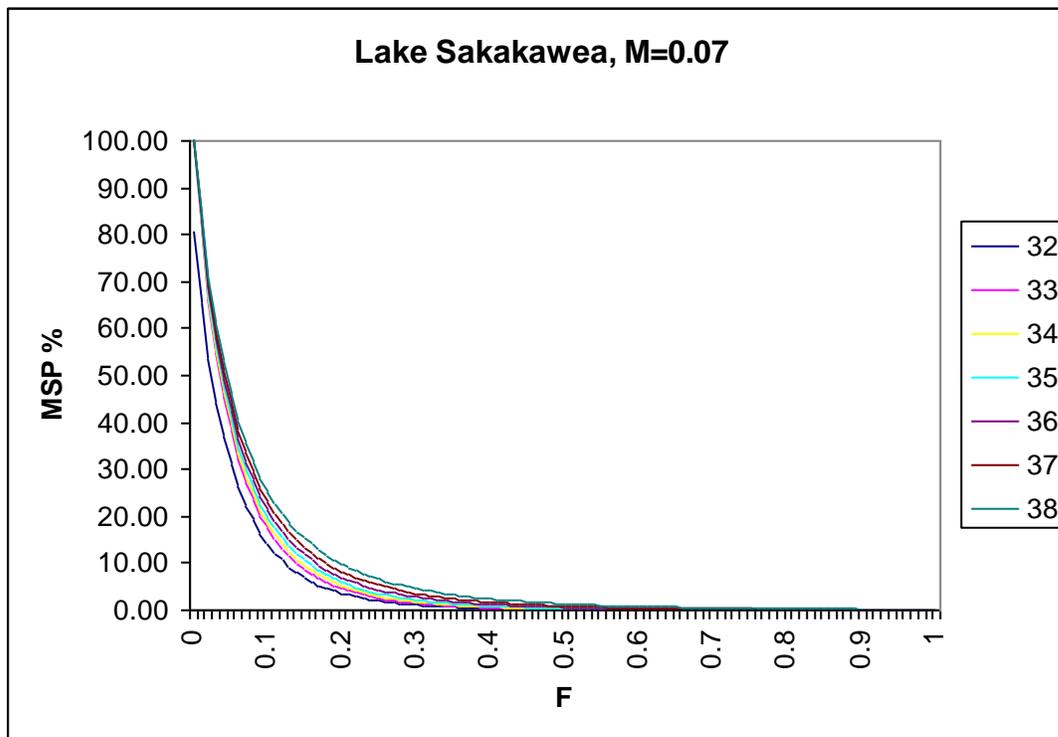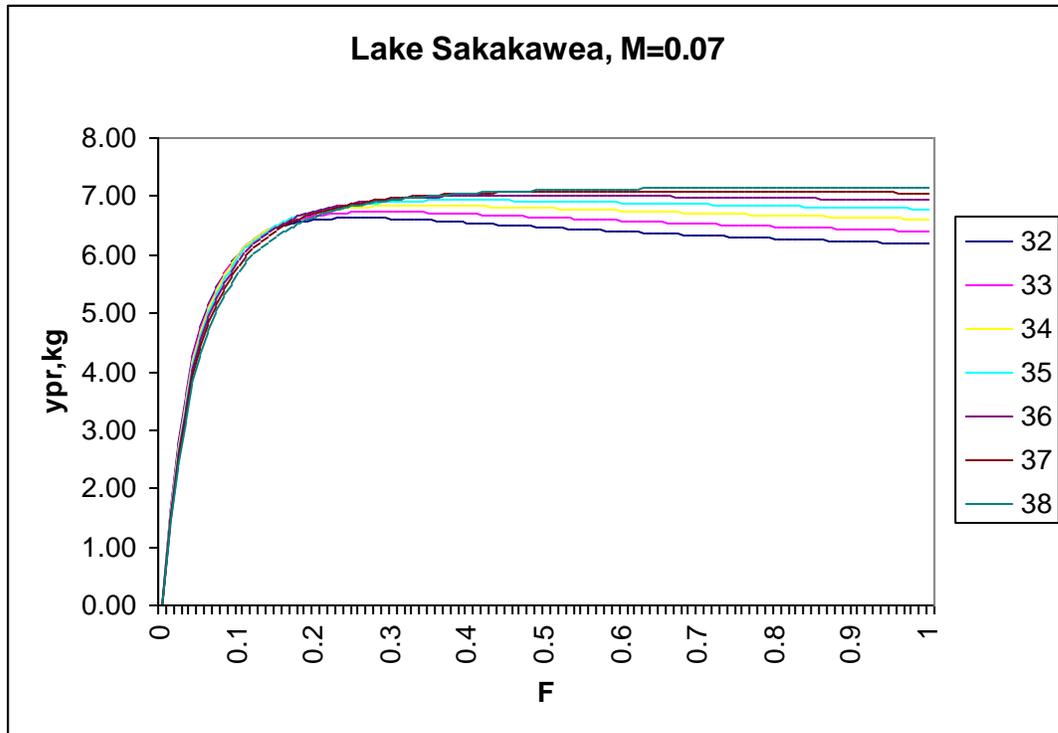
Figure 3.1.2. Yield per recruit (upper panel) and percent MSP (lower panel) for Lake Sakakawea, North Dakota Paddlefish at various minimum legal sizes (inches).
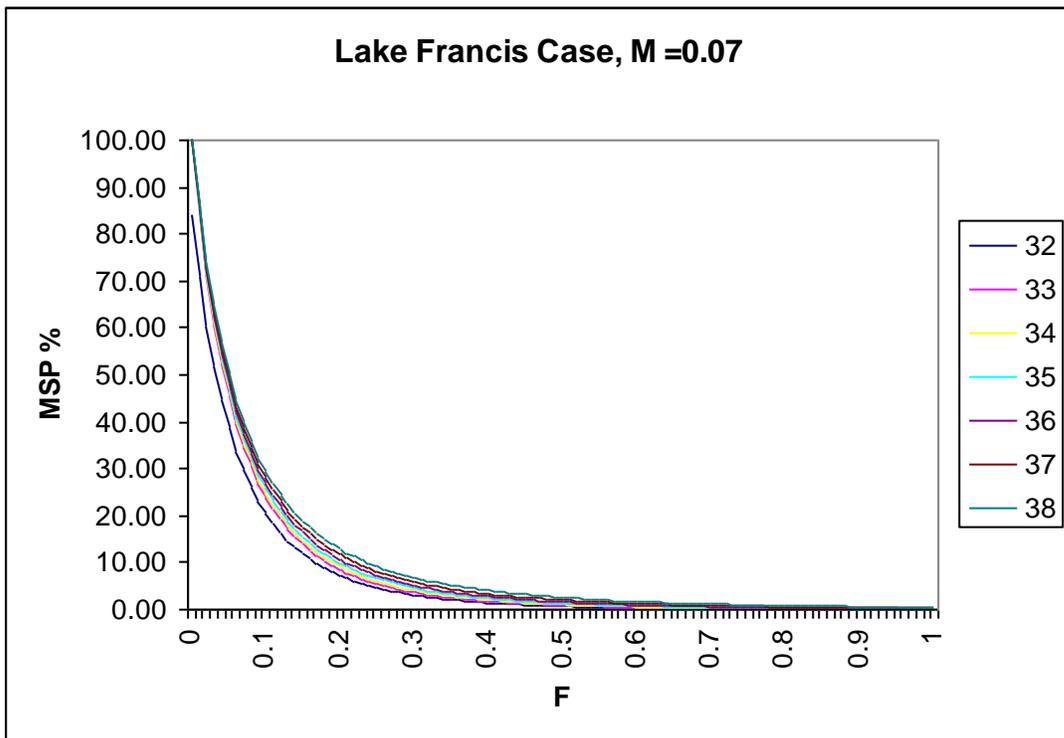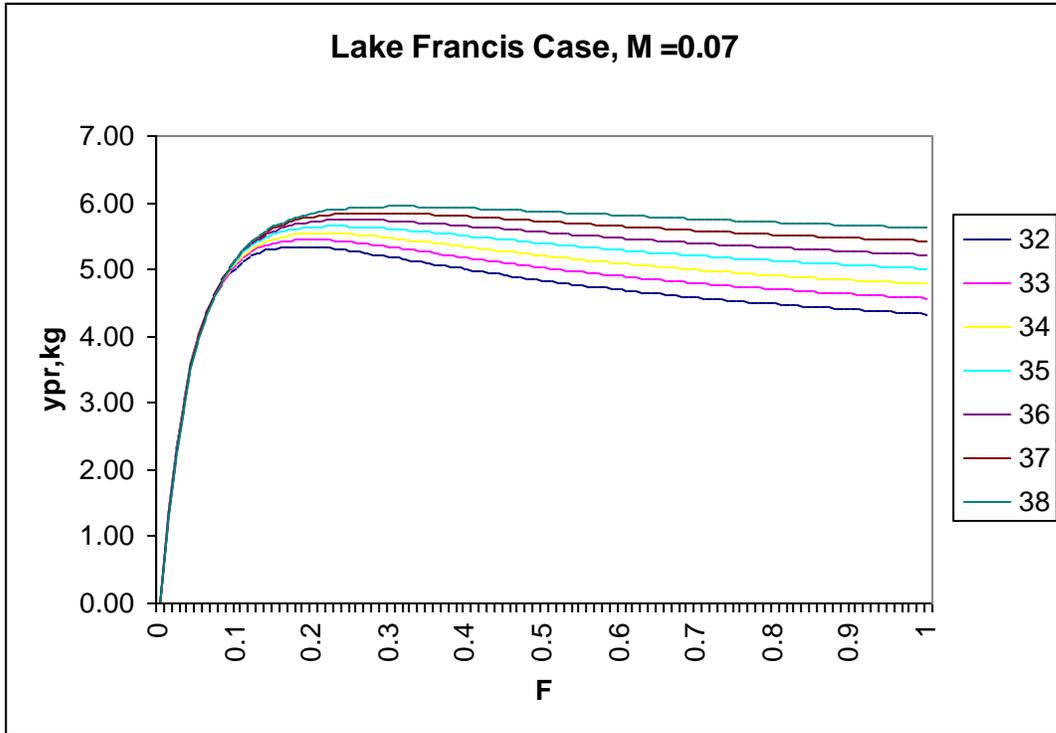
Figure 3.1.3. Yield per recruit (upper panel) and percent MSP (lower panel) for Lake Francis Case, South Dakota Paddlefish at various minimum legal sizes (inches). Natural mortality M=0.07.
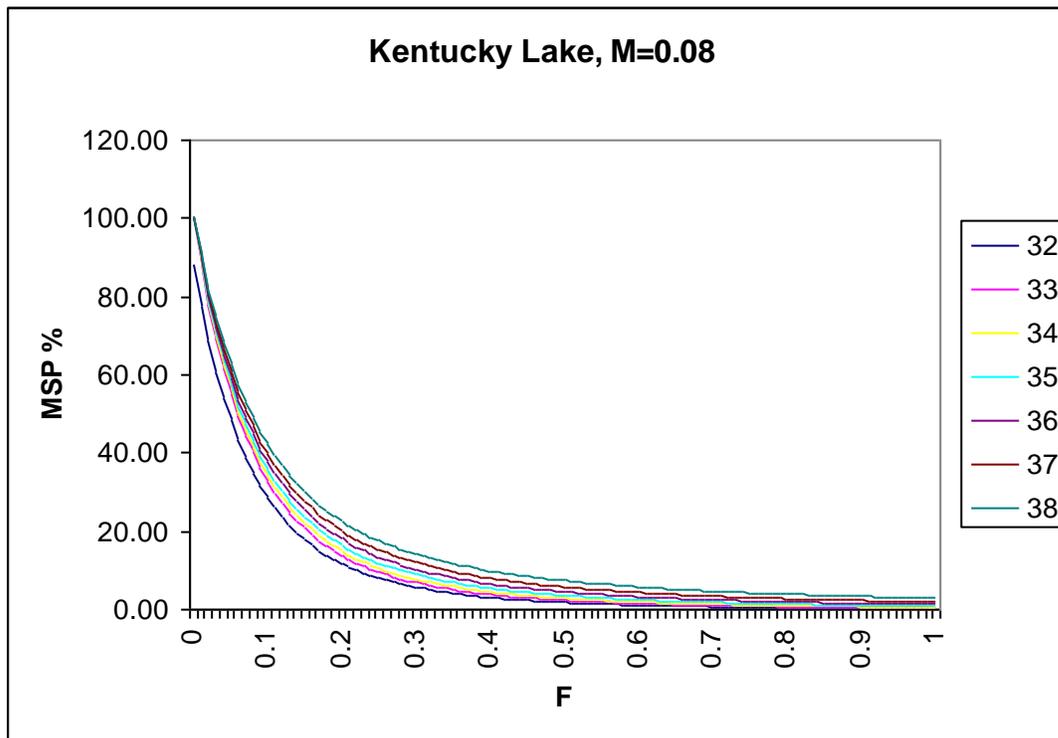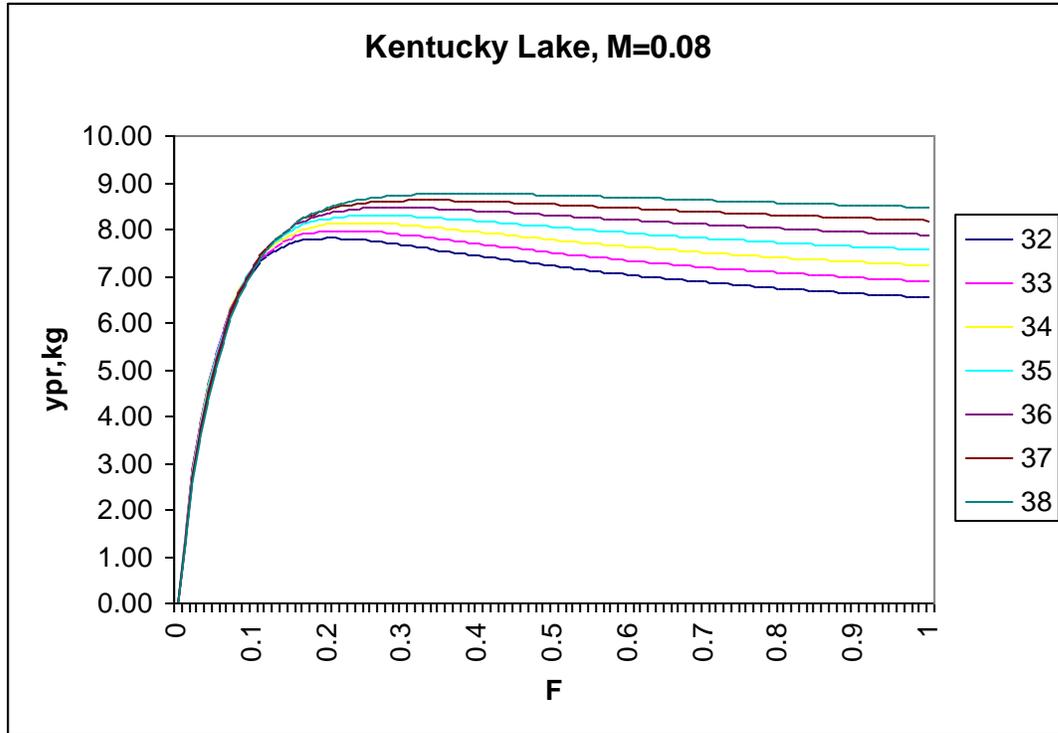
Figure 3.1.4. Yield per recruit (upper panel) and percent MSP (lower panel) for Kentucky Lake Paddlefish at various minimum legal sizes (inches). Natural mortality M=0.08.
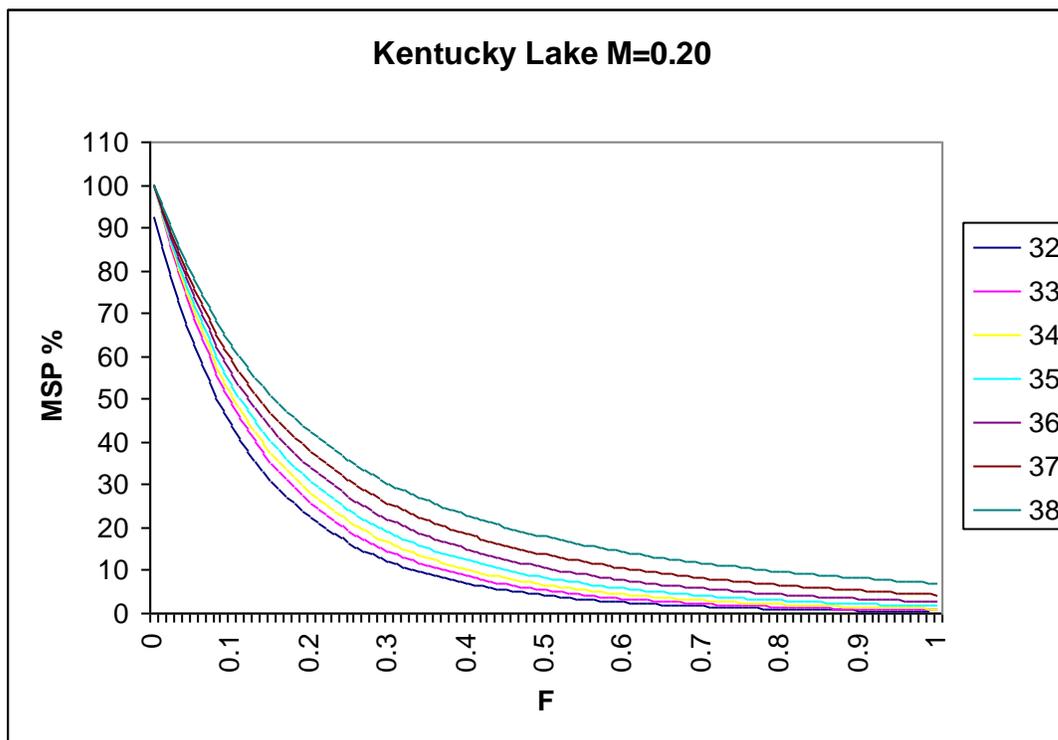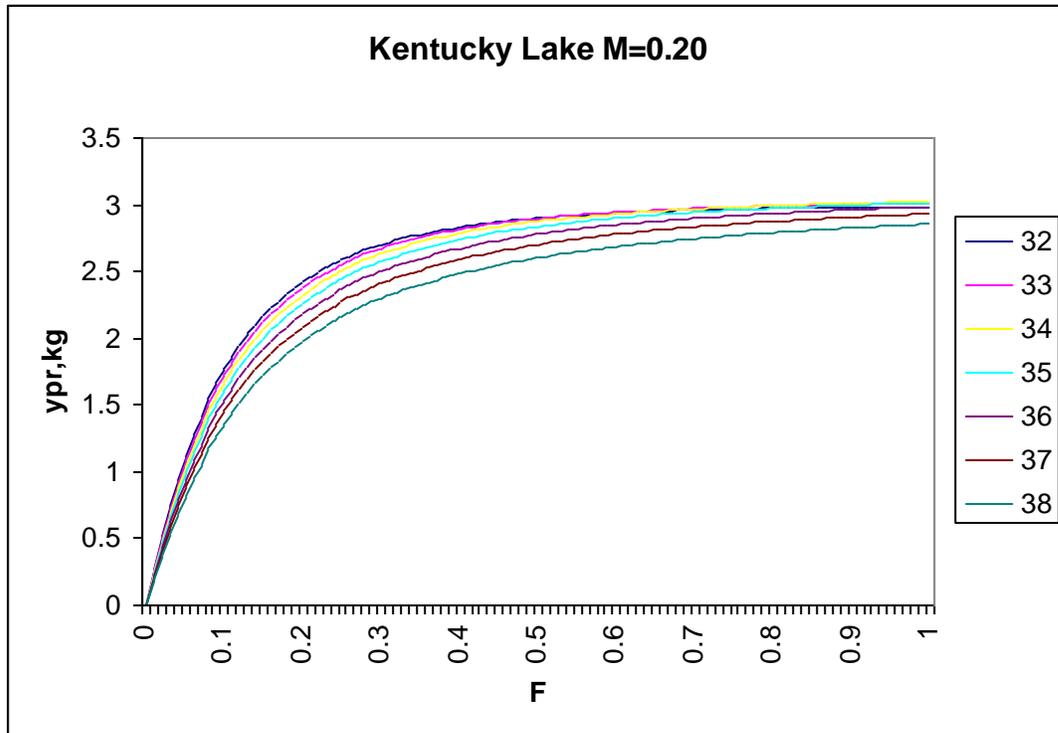
Figure 3.1.5. Yield per recruit (upper panel) and percent MSP (lower panel) for Kentucky Lake, Tennessee Paddlefish at various minimum legal sizes (inches). Natural mortality M=0.20.
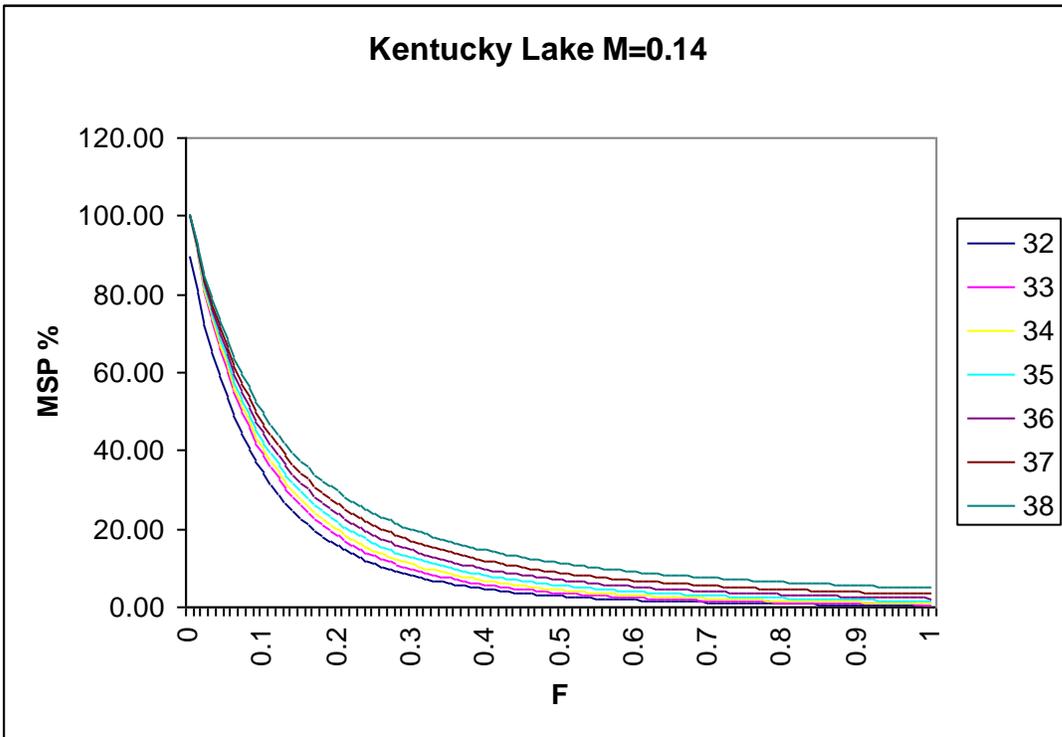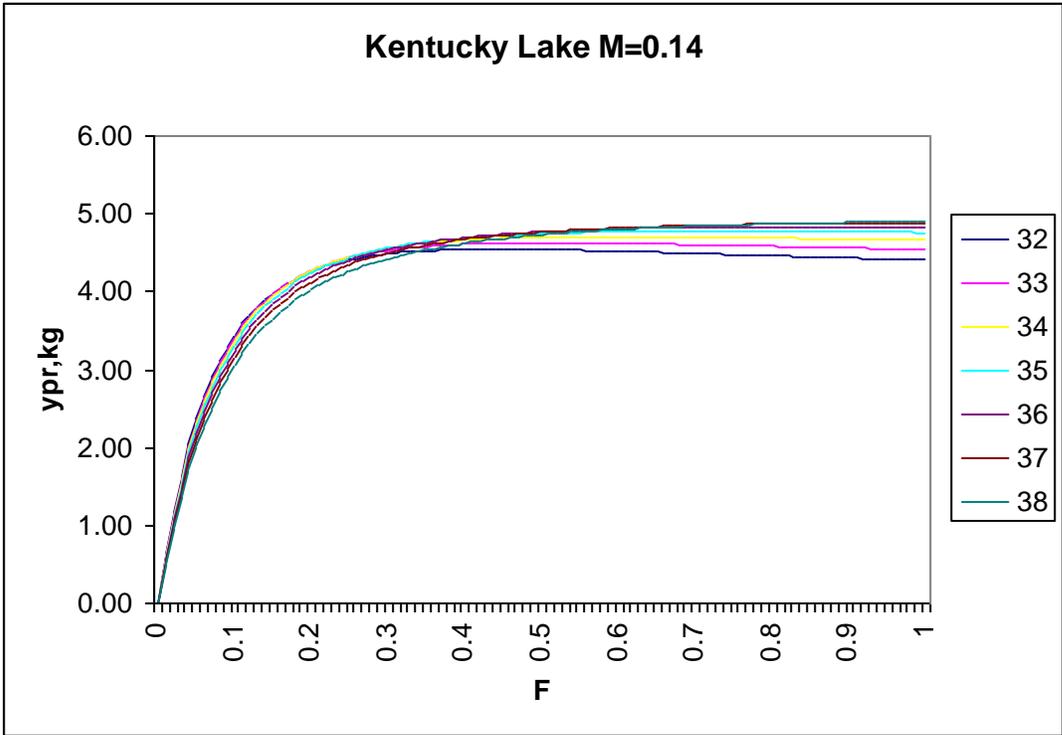
Figure 3.1.6. Yield per recruit (upper panel) and percent MSP (lower panel) for Kentucky Lake, Tennessee Paddlefish at various minimum legal sizes (inches). Natural mortality M=0.14.
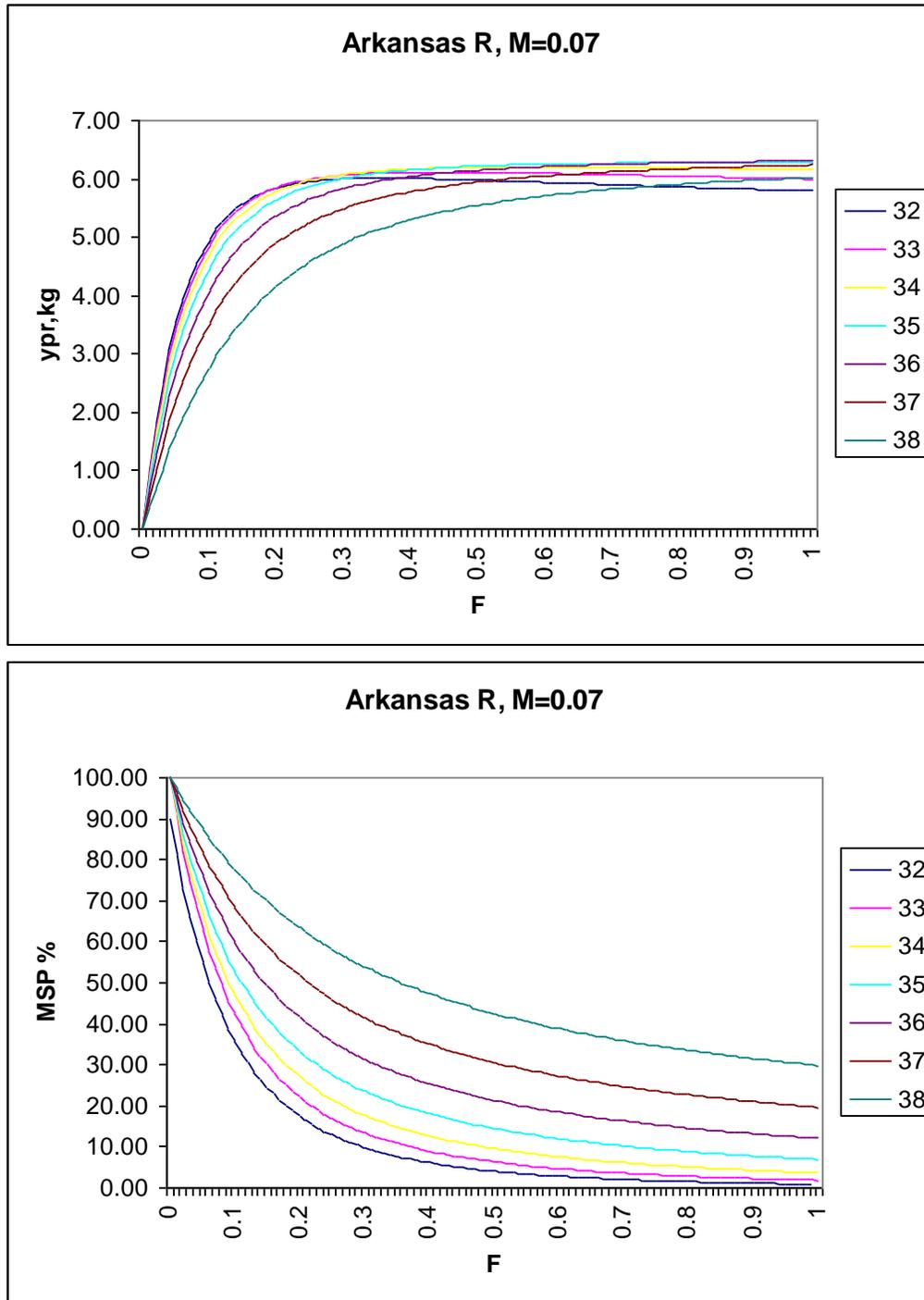
Figure 3.1.7. Yield per recruit (upper panel) and percent MSP (lower panel) for Arkansas River, Arkansas Paddlefish at various minimum legal sizes (inches). Natural mortality M=0.07.

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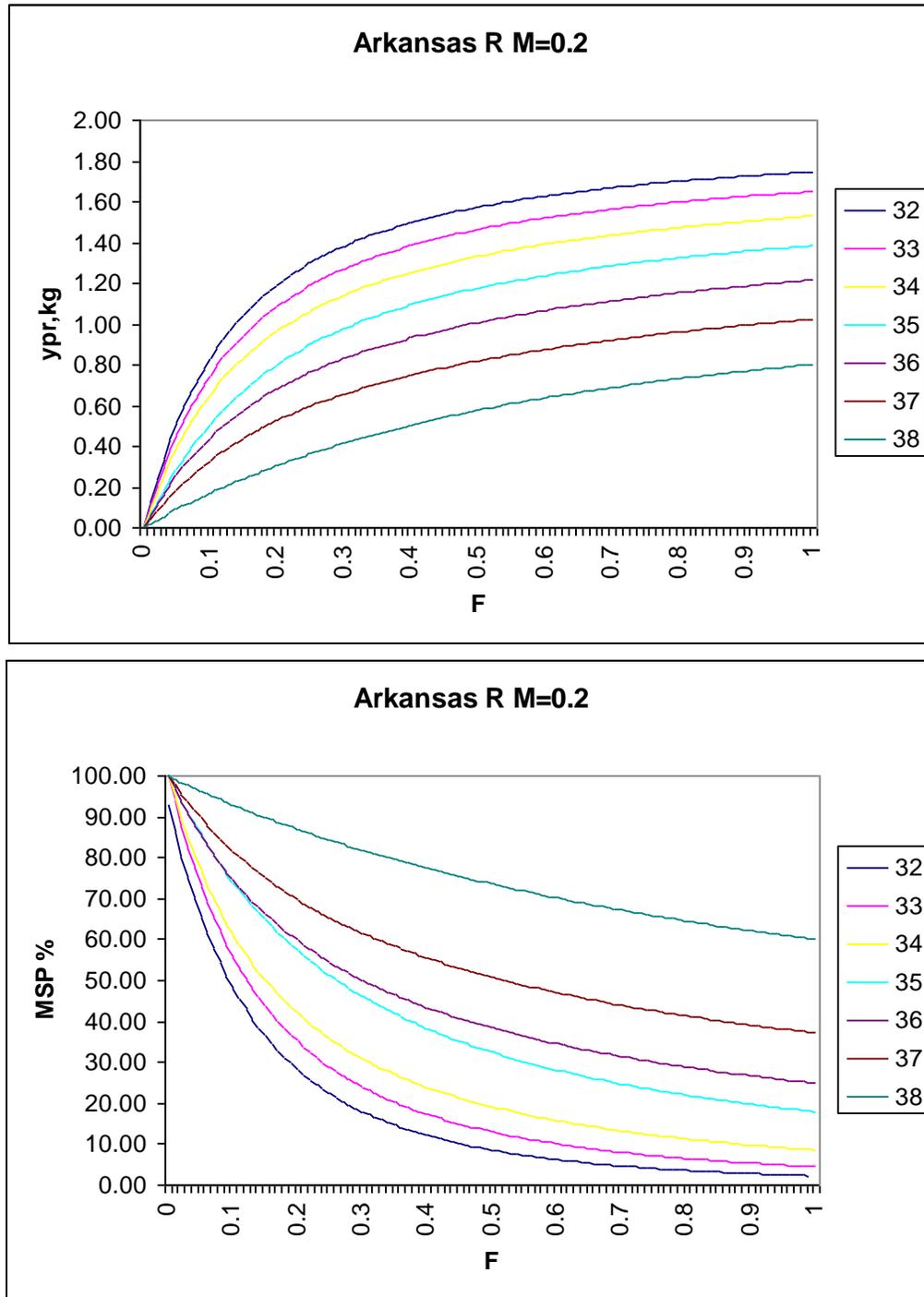
Figure 3.1.8. Yield per recruit (upper panel) and percent MSP (lower panel) for Arkansas River, Arkansas Paddlefish at various minimum legal sizes (inches). Natural mortality M=0.20.
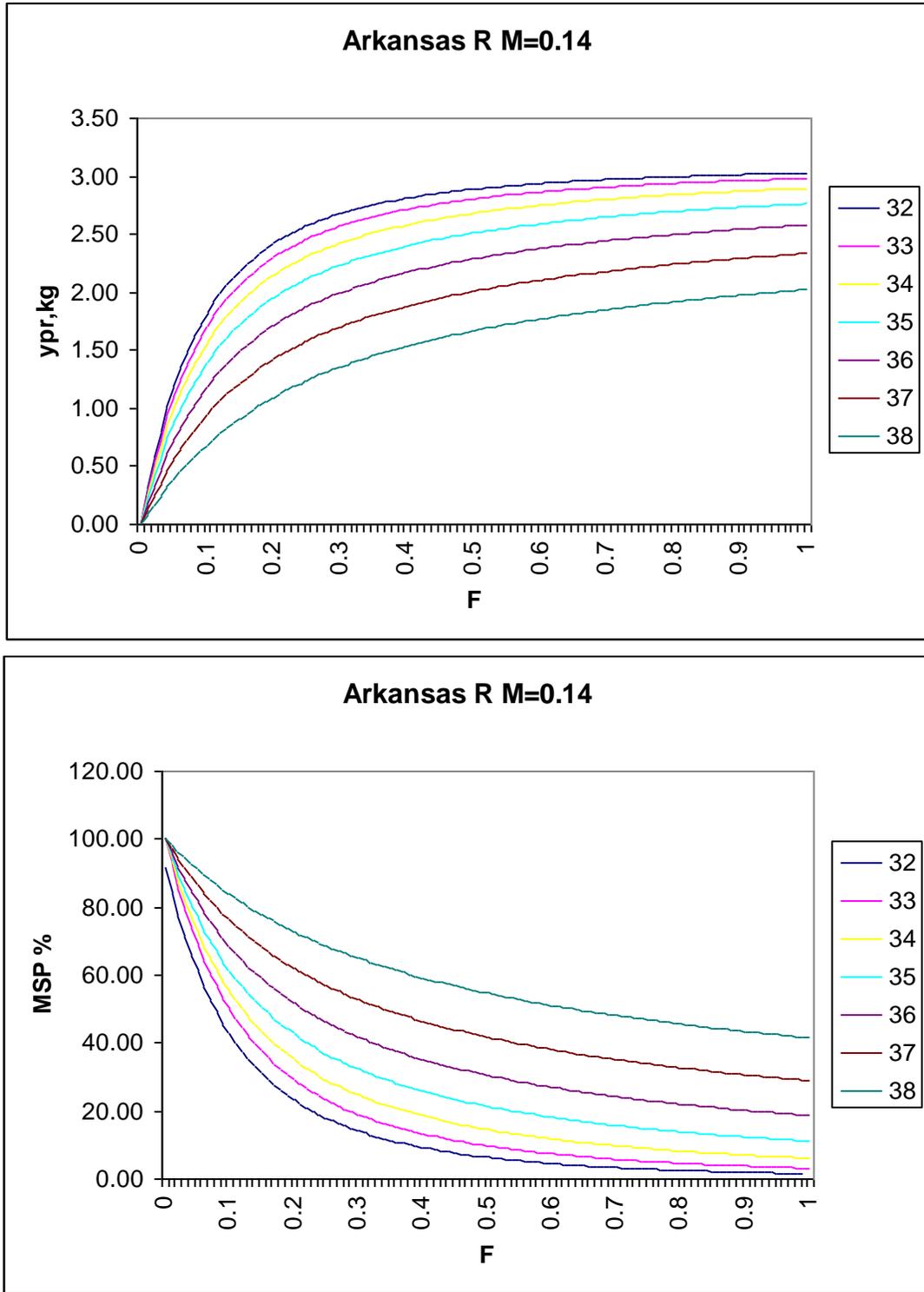
Figure 3.1.9. Yield per recruit (upper panel) and percent MSP (lower panel) for Arkansas River, Arkansas Paddlefish at various minimum legal sizes (inches). Natural mortality M=0.14.
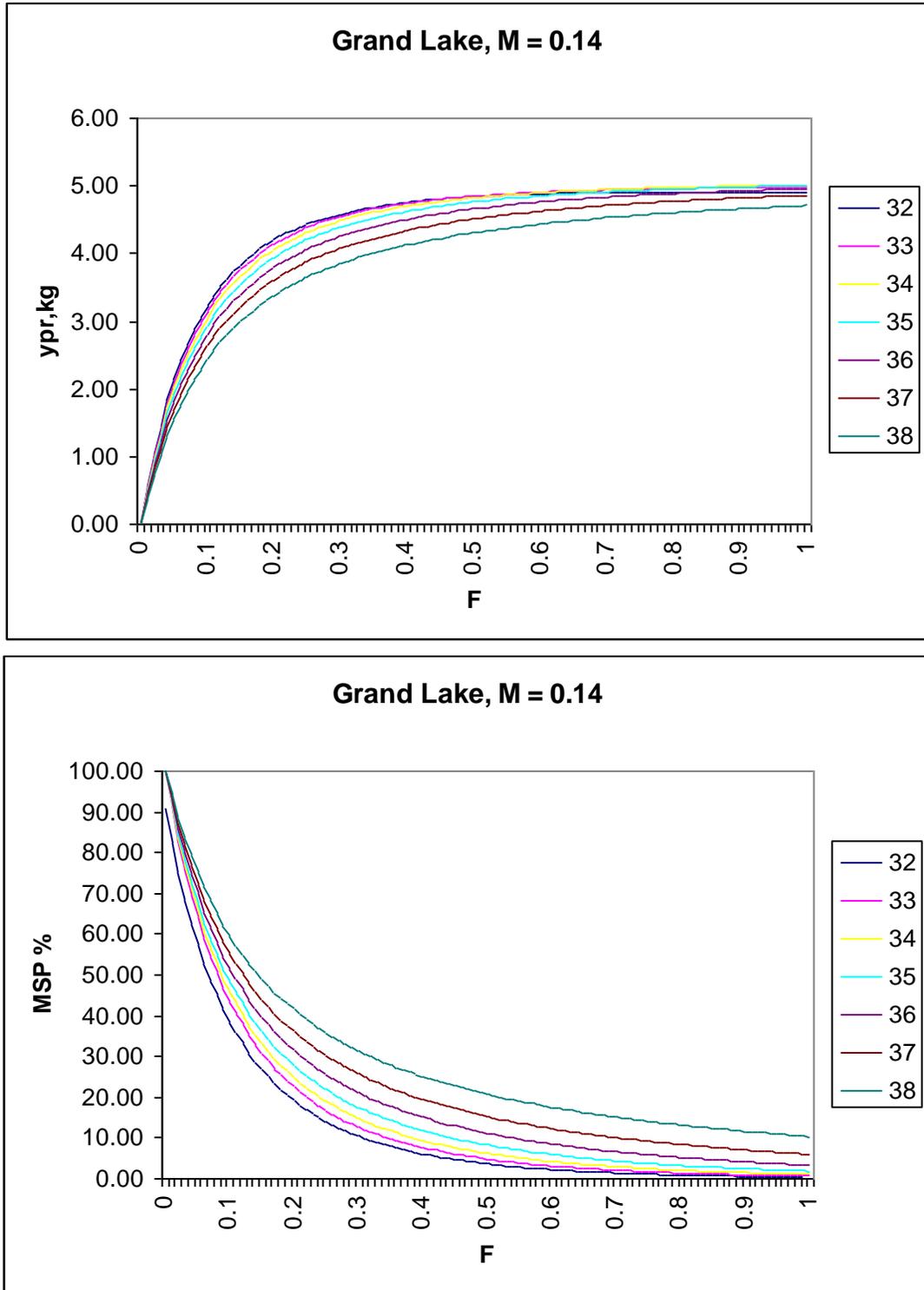
Figure 3.1.10. Yield per recruit (upper panel) and percent MSP (lower panel) for Grand Lake, Oklahoma Paddlefish at various minimum legal sizes (inches). Natural mortality M=0.14.
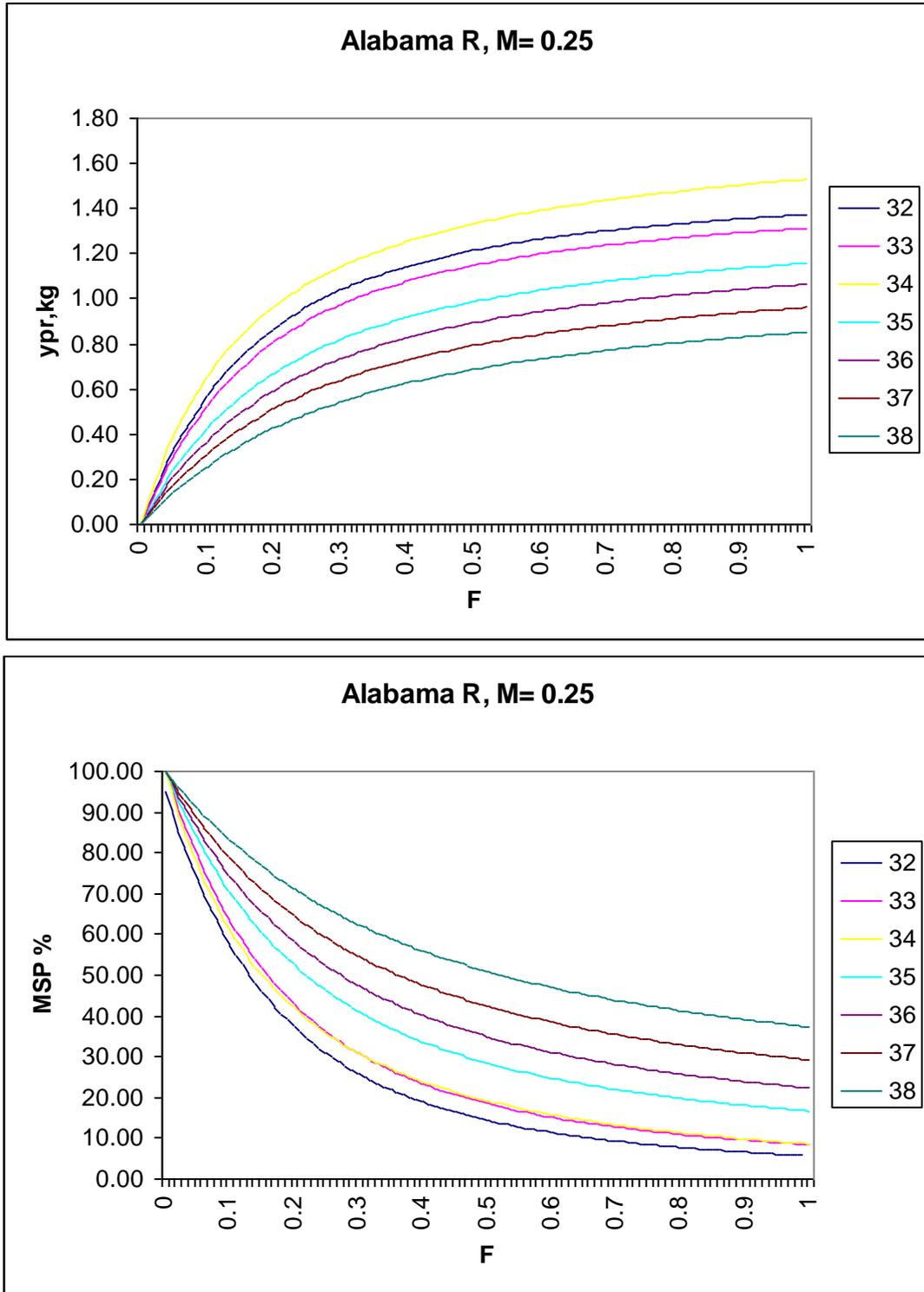
Figure 3.1.11. Yield per recruit (upper panel) and percent MSP (lower panel) for Alabama River, Alabama Paddlefish at various minimum legal sizes (inches). Natural mortality M=0.25.
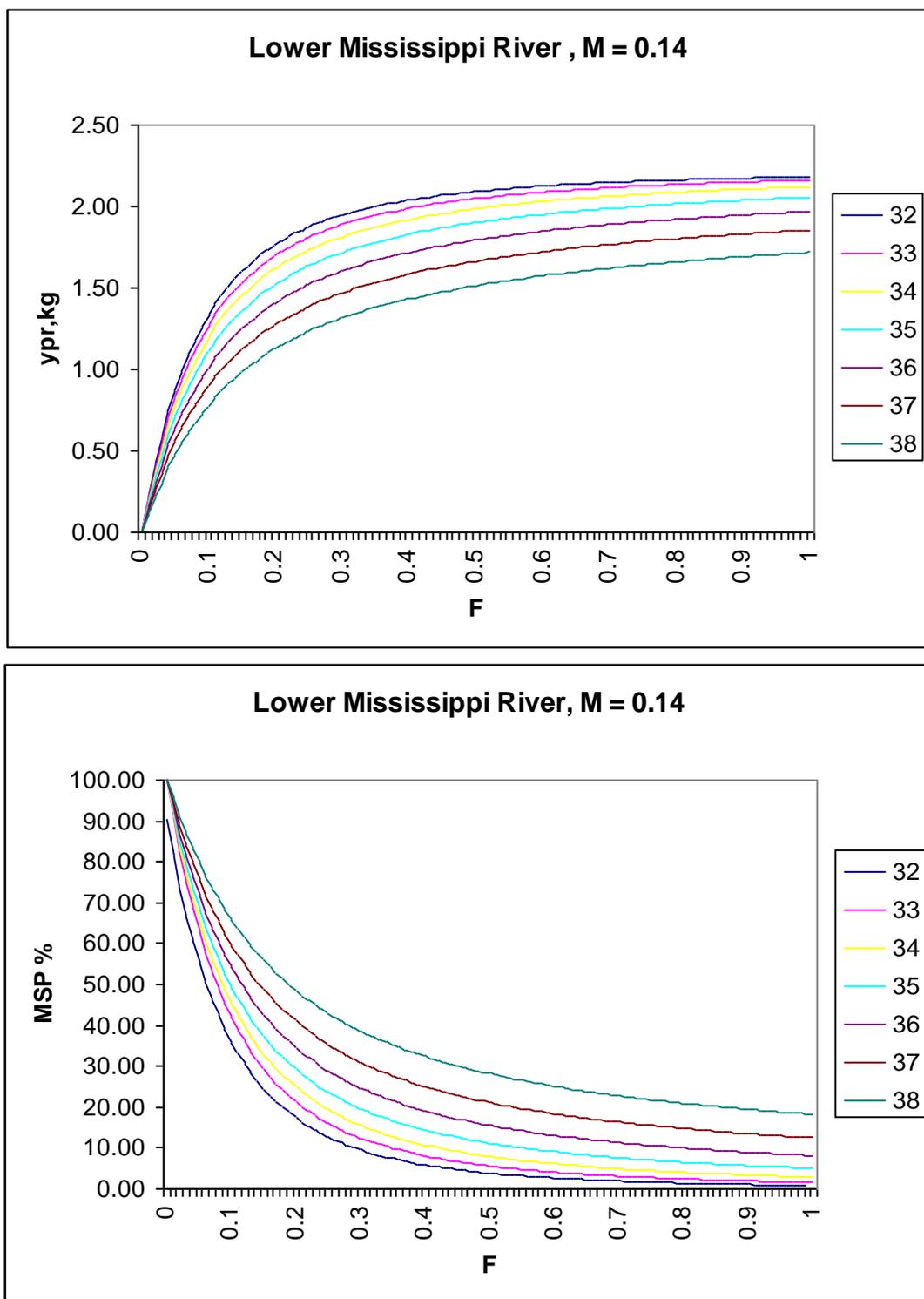
Figure 3.1.12. Yield per recruit (upper panel) and percent MSP (lower panel) for Lower Mississippi River Paddlefish at various minimum legal sizes (inches).Natural mortality M=0.14.
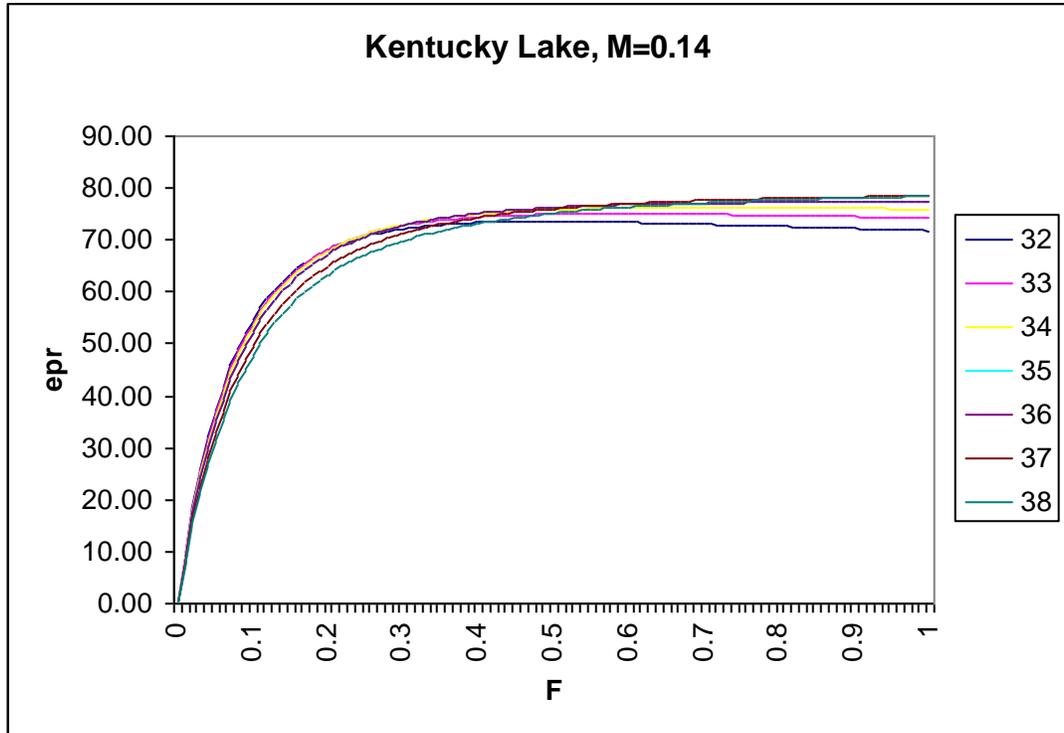
Figure 3.1.13. Egg per recruit for Kentucky Lake, Tennessee Paddlefish at various minimum legal sizes (inches).Natural mortality M=0.14.
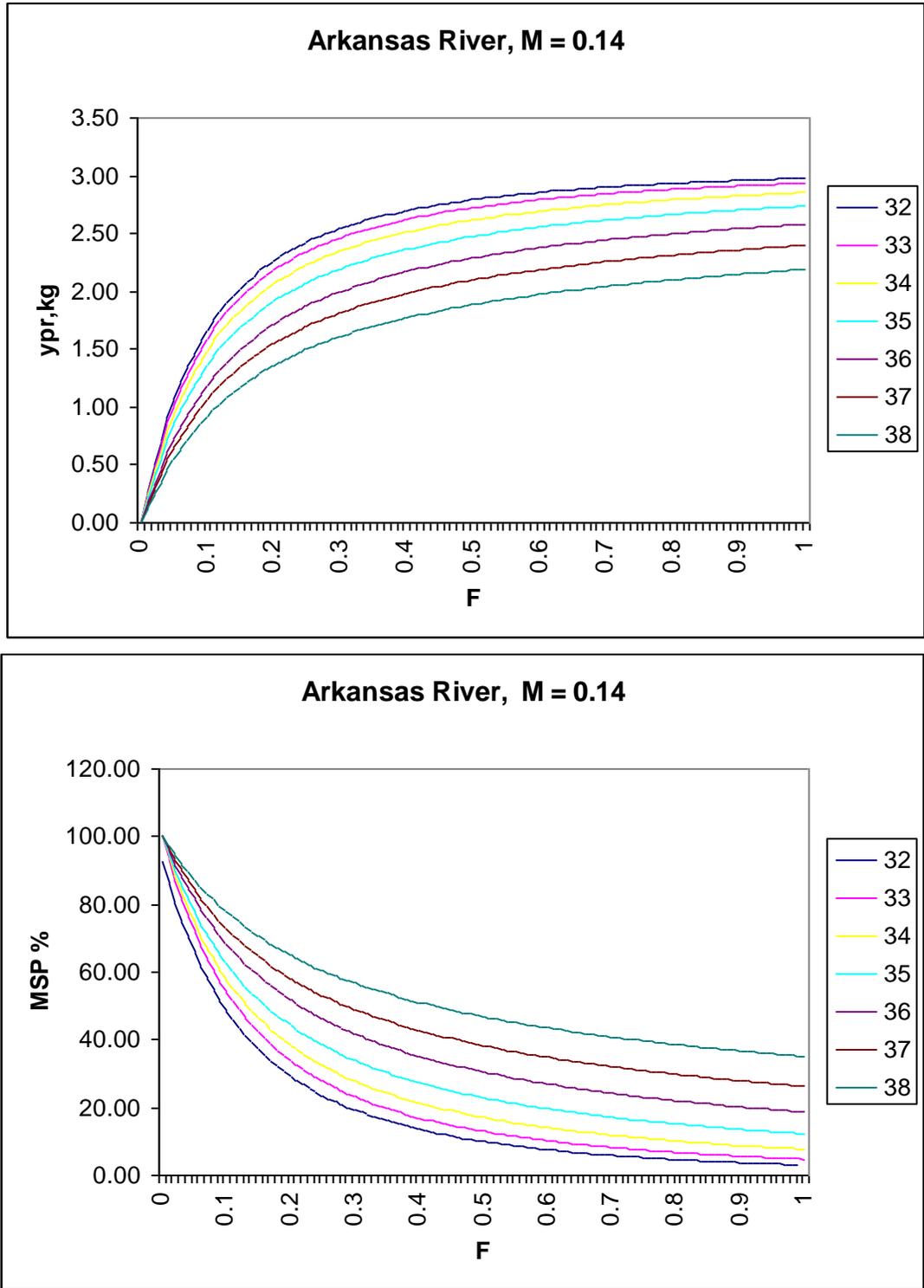
Figure 3.1.14. Yield per recruit (upper panel) and percent MSP (lower panel) for Arkansas River Paddlefish at various minimum legal sizes (inches) with correction for gillnet selectivity. Natural mortality M=0.14.
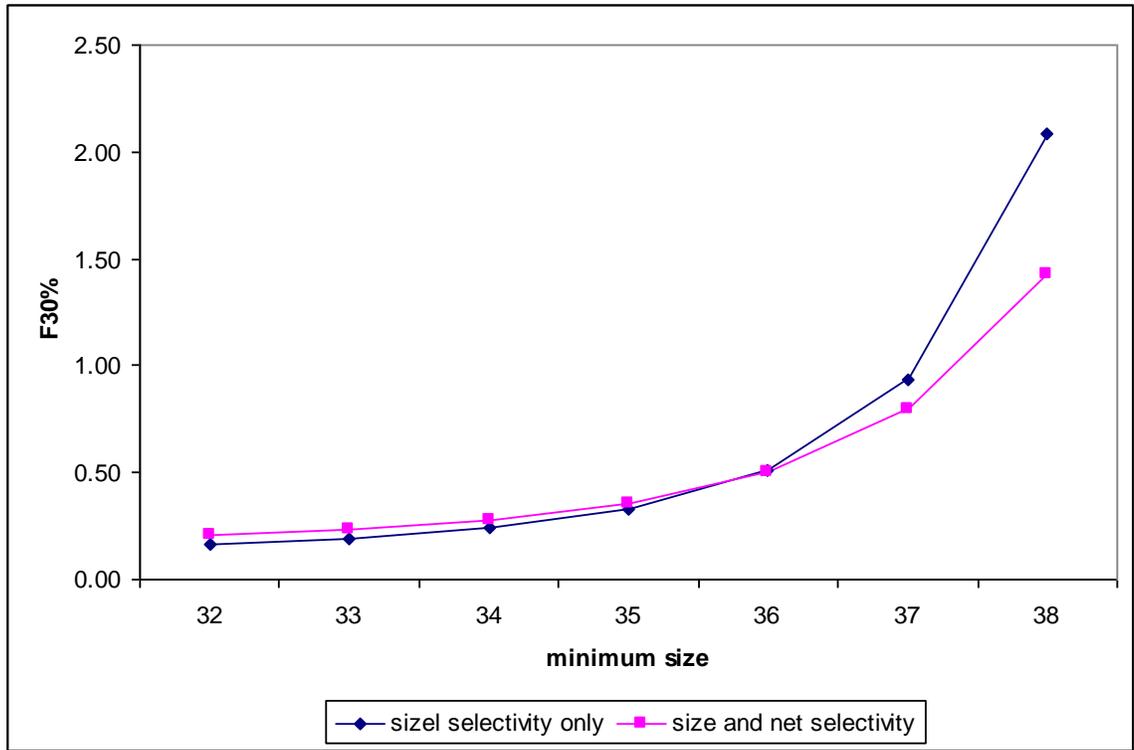
Figure 3.1.15. F30% SPR based on minimum size with and without gillnet selectivity correction for Arkansas River, Arkansas Paddlefish.
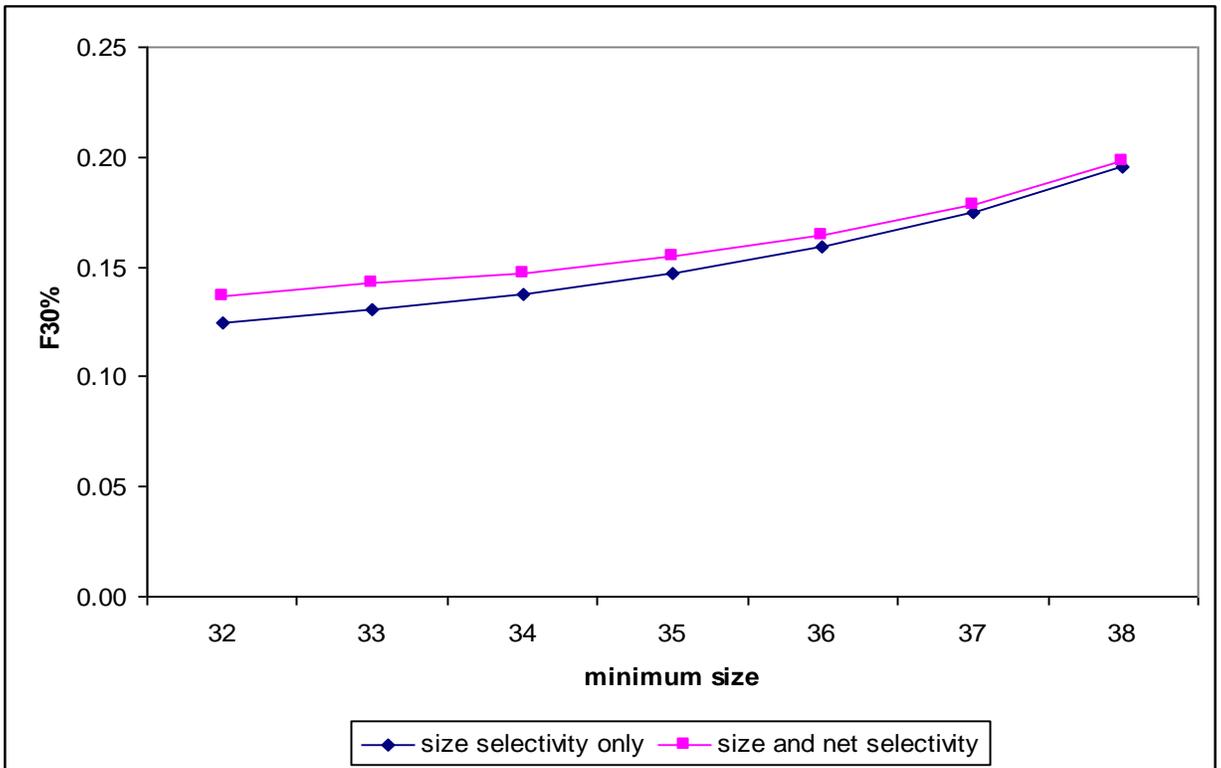
Figure 3.1.16. F30% SPR based on minimum size with and without gillnet selectivity correction for Kentucky Lake, Tennessee Paddlefish.
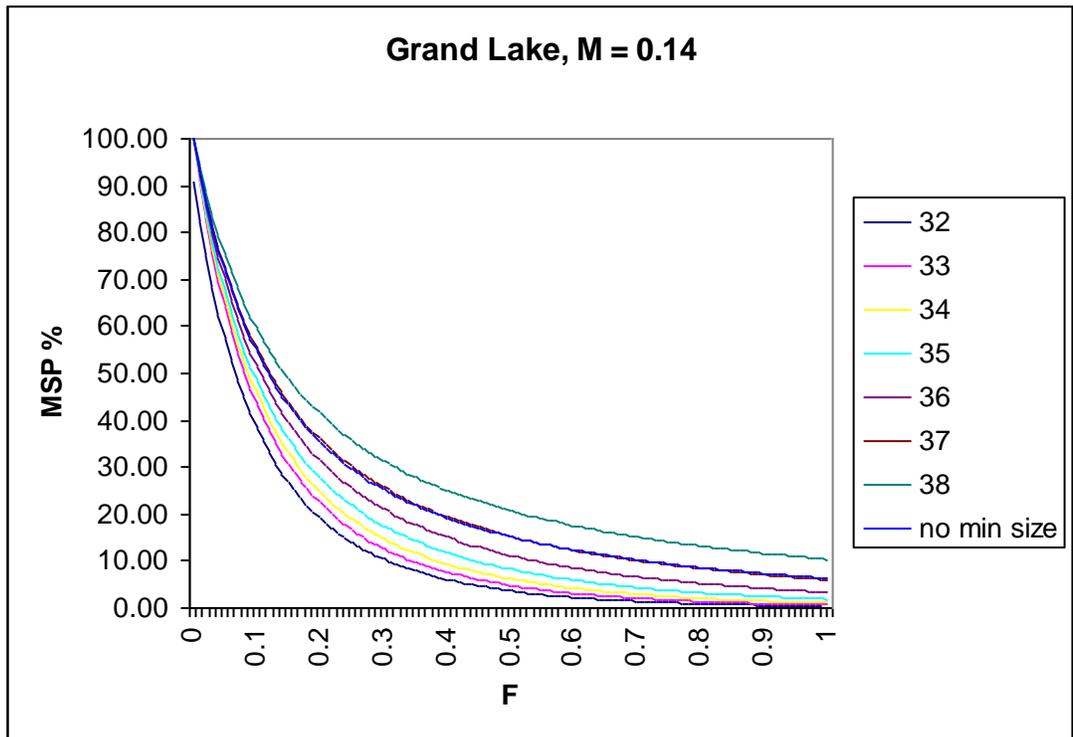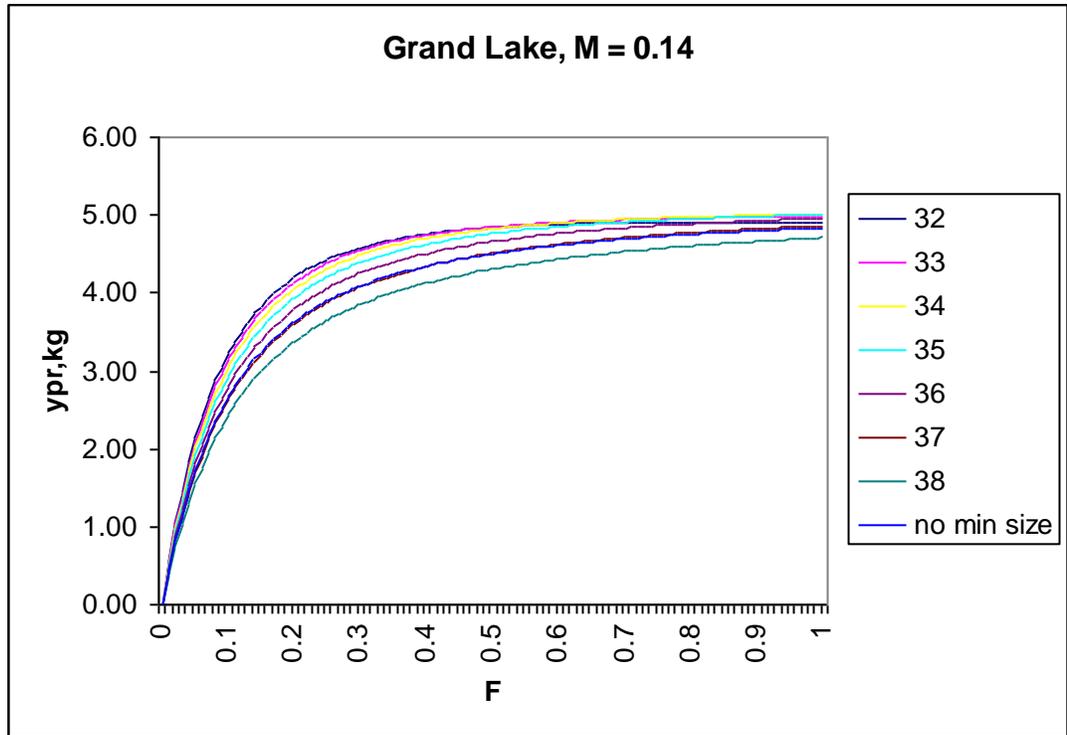
Figure 3.1.17. Yield per recruit (upper panel) and percent MSP (lower panel) for Grand Lake, Oklahoma Paddlefish with various minimum length sizes (inches).

Lake Sakakawea, M=0.07

Lake Sakakawea, M=0.07
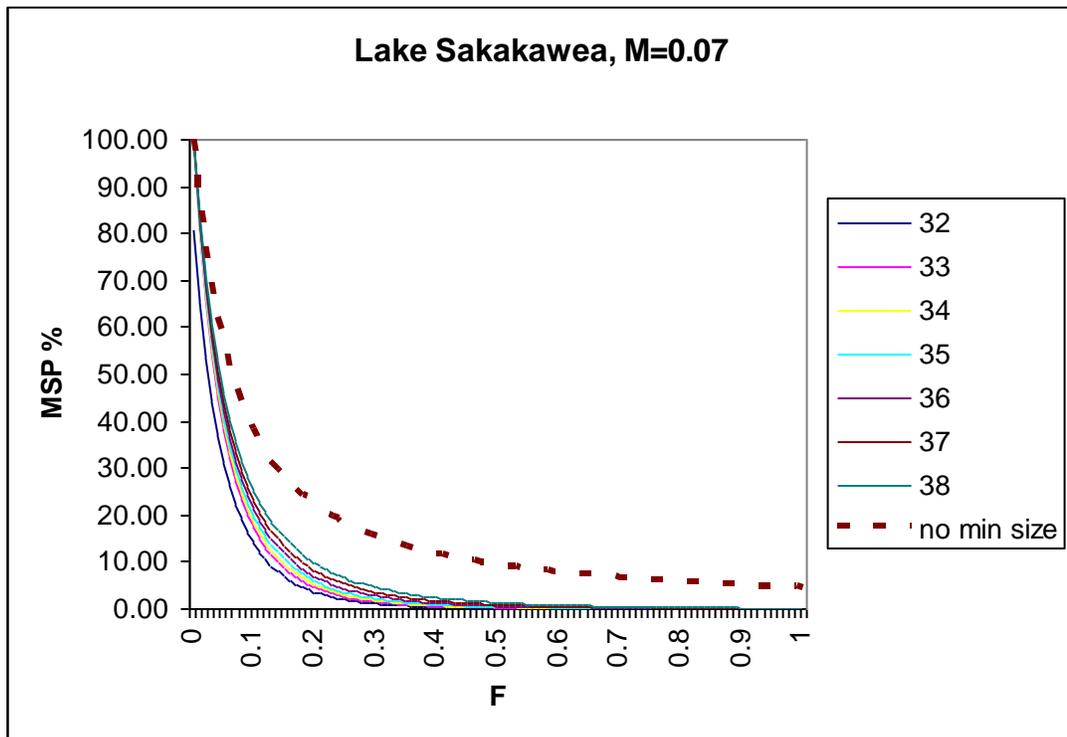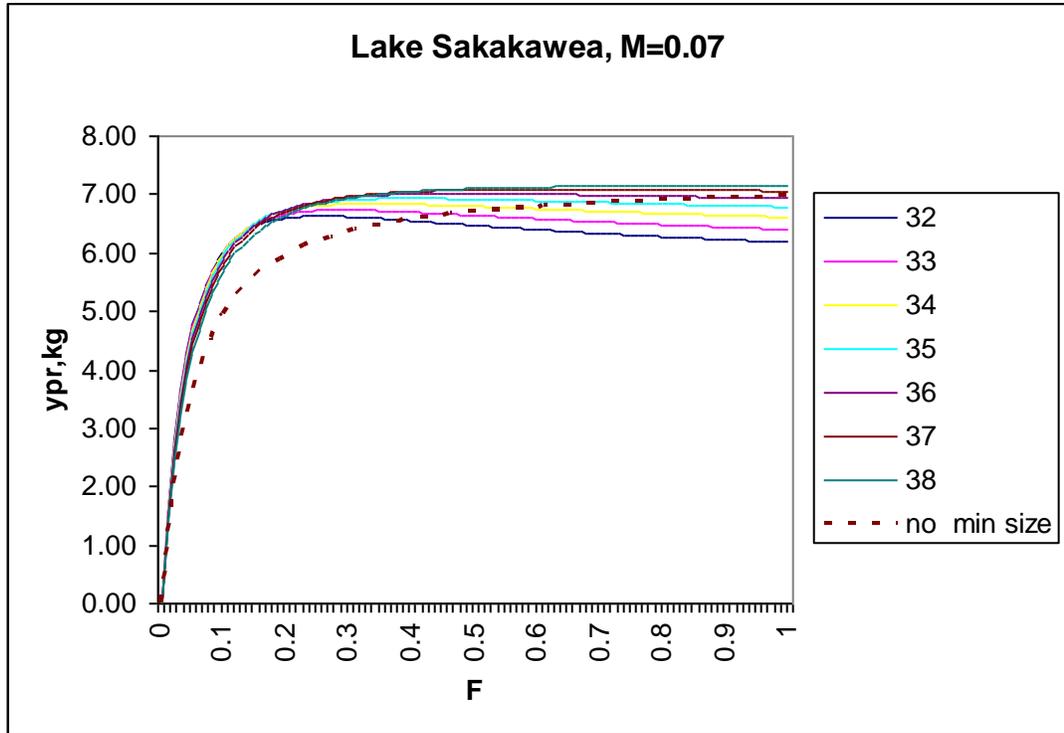
Figure 3.1.18. Yield per recruit (upper panel) and percent MSP (lower panel) for Lake Sakakawea, North Dakota Paddlefish with now minimum size (dashed line) and various minimum length sizes (inches).
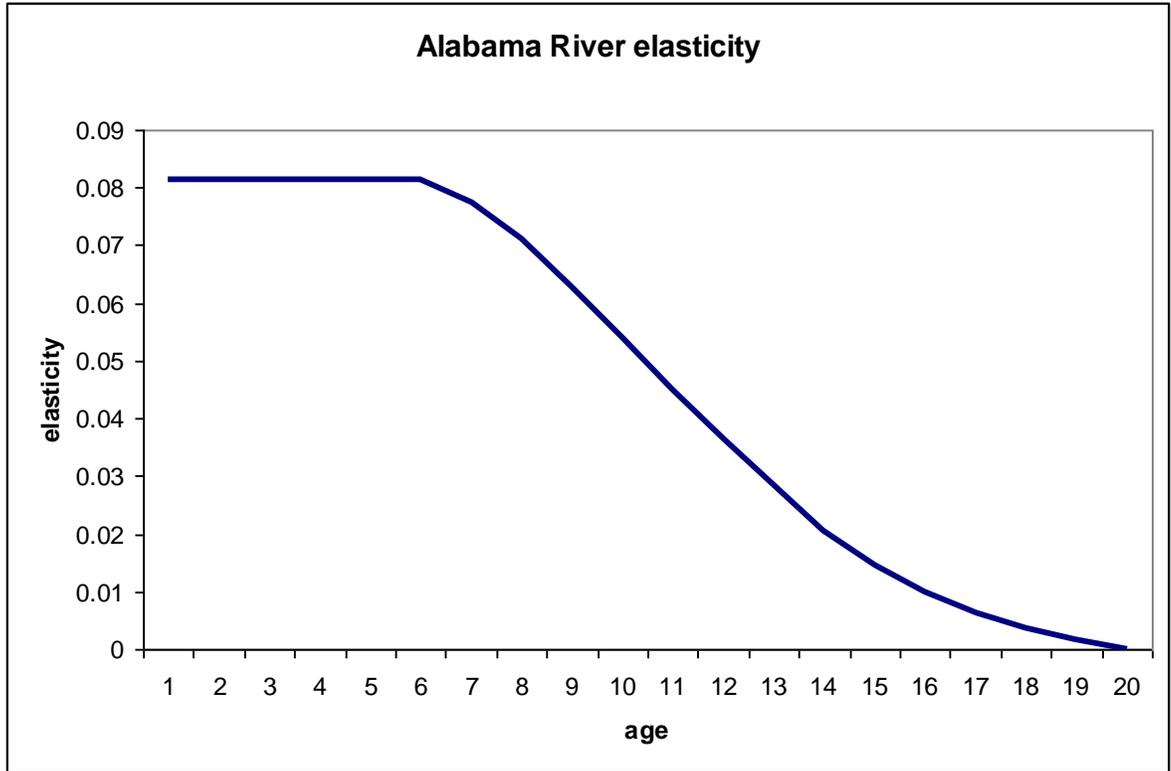
Figure 3.6.1. Elasticity for Alabama River, Alabama stock with 20 age classes and M=0.3.
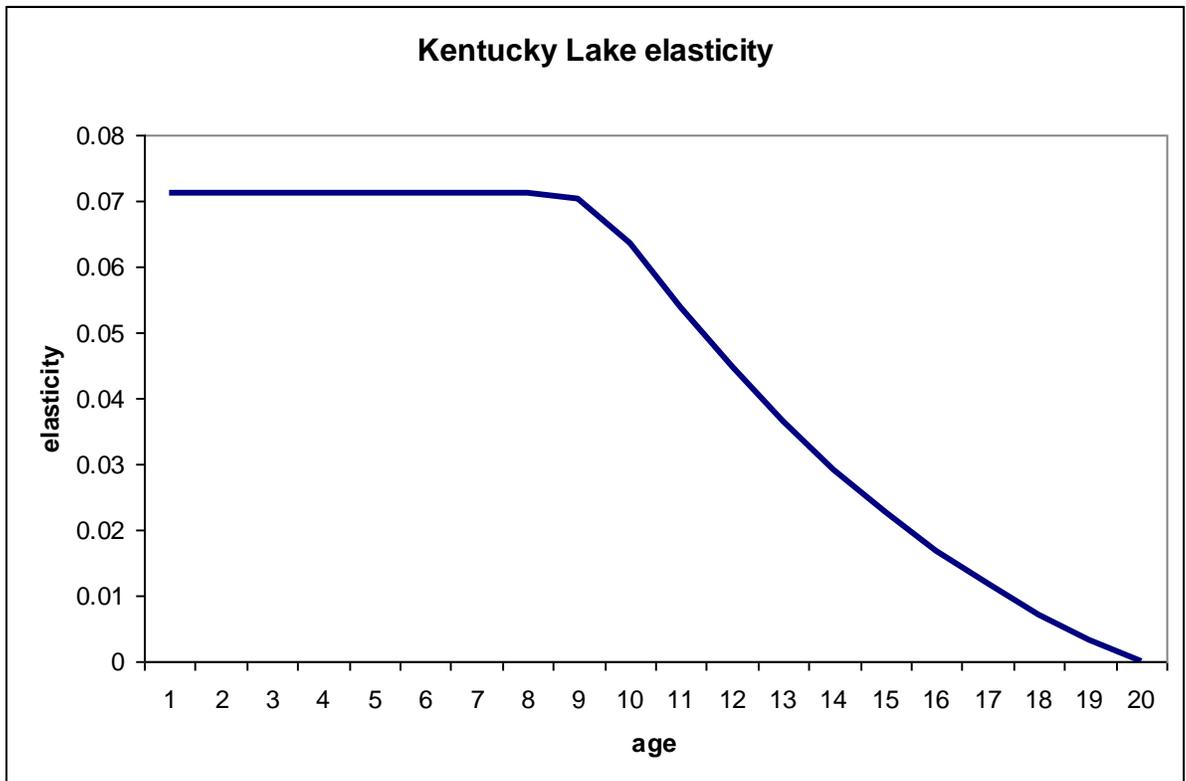
Figure 3.6.2. Elasticity for Kentucky Lake, Tennessee Paddlefish population with 20 age classes, M=0.17.
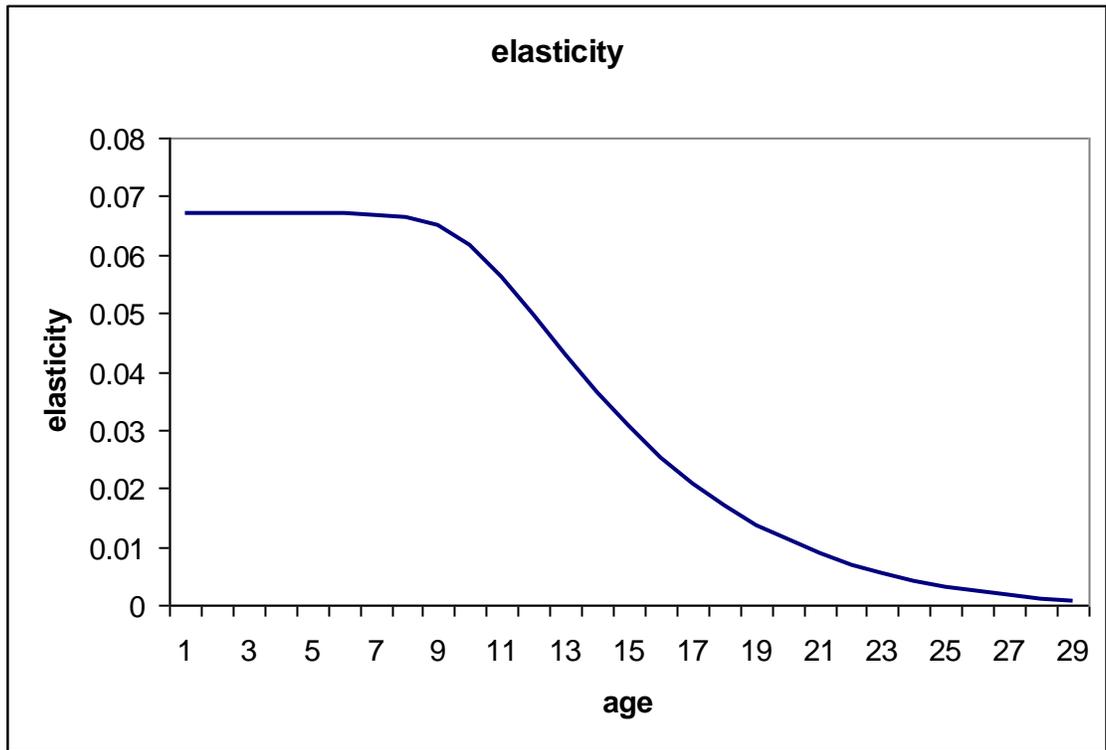
Figure 3.6.3. Elasticity for Kentucky Lake Paddlefish population with 30 age classes, M=0.14.
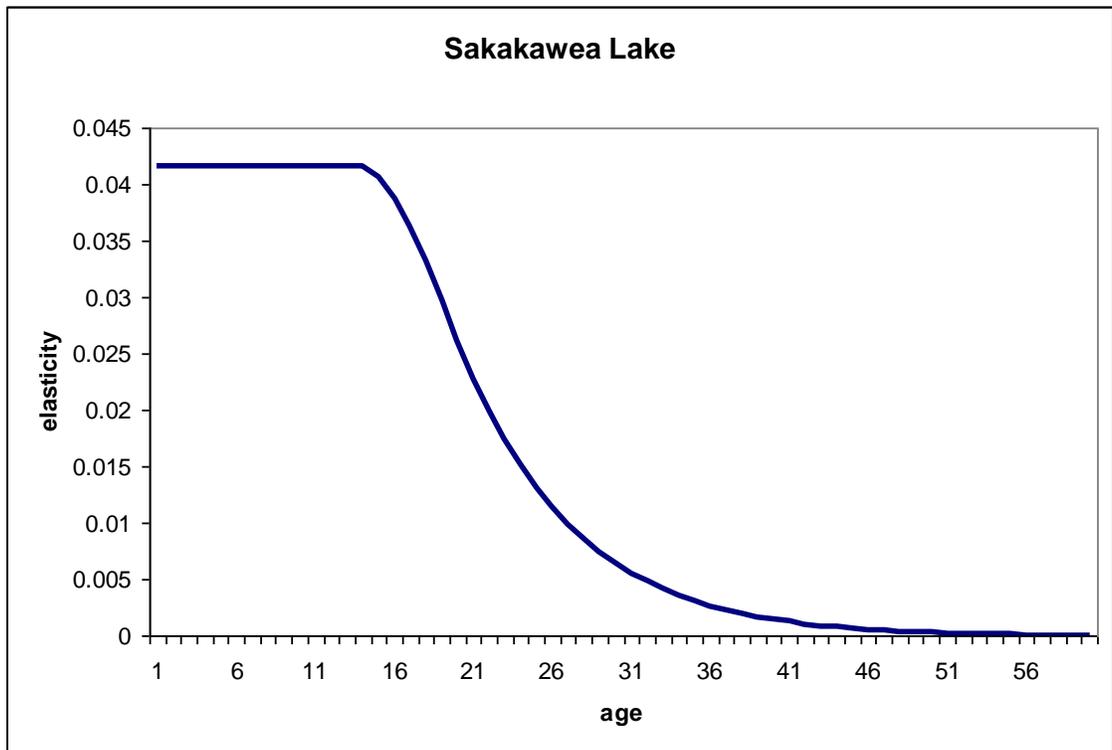
Figure 3.6.4. Elasticity for Sakakawea Lake North Dakota Paddlefish population with 60 age classes, M=0.07.
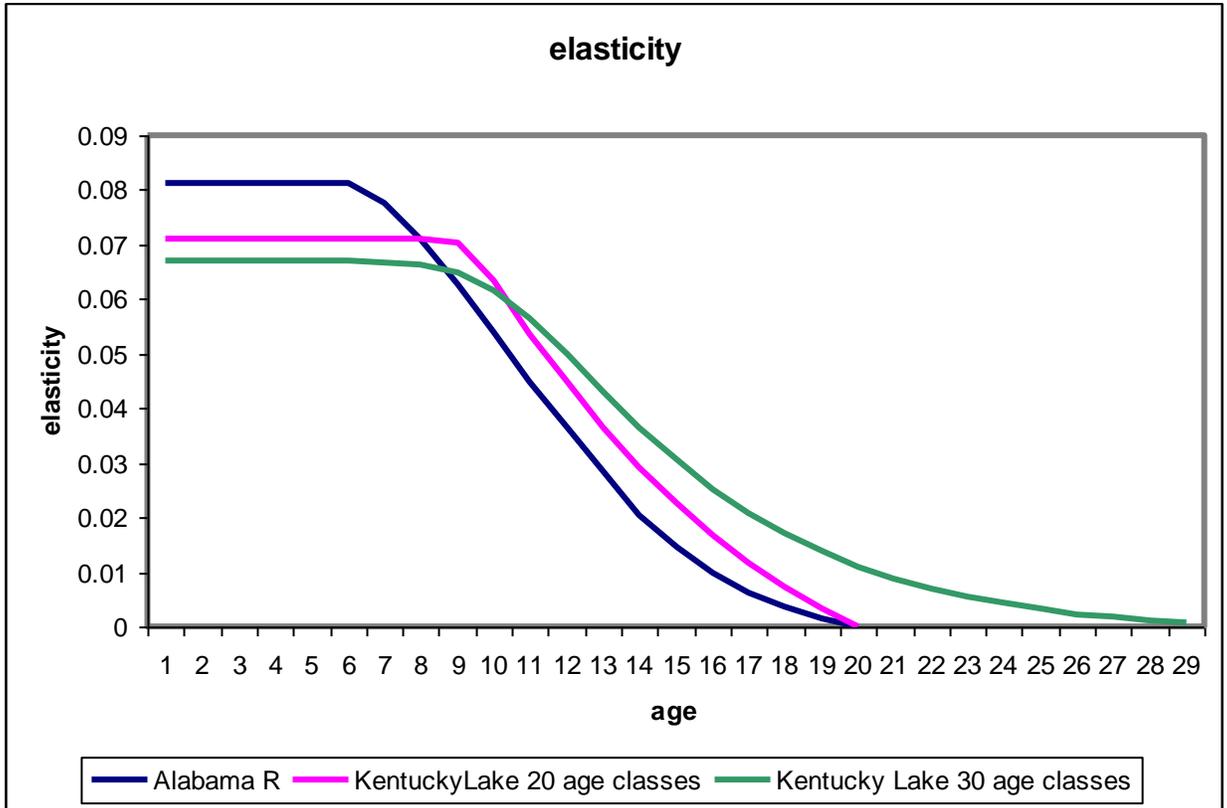
Figure 3.6.5. Elasticity comparison among analyzed stocks.
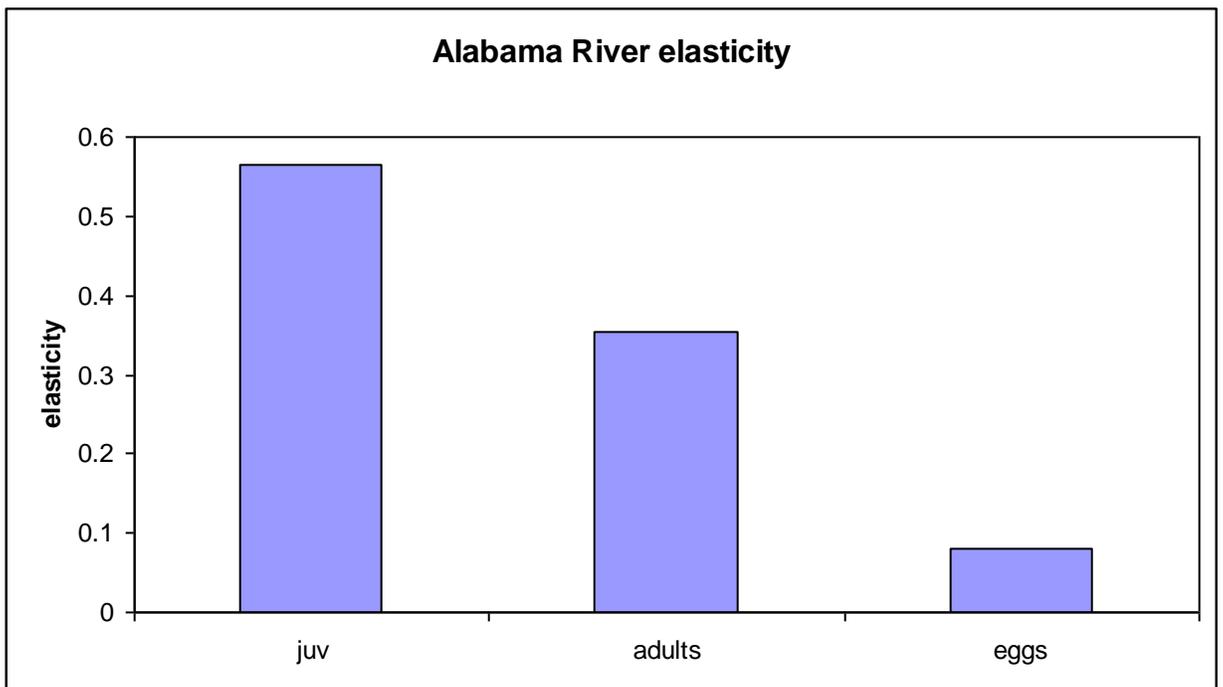
Figure 3.6.6. Cumulative elasticity effect by for egg, juvenile and adults stages of Alabama River, Alabama population (20 age groups).
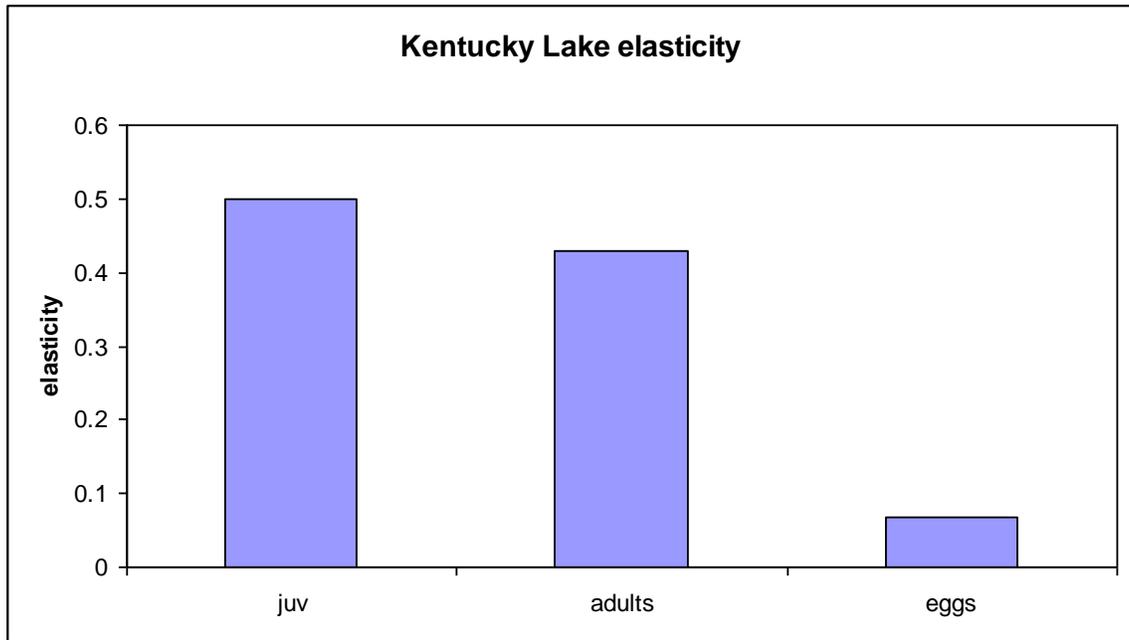
Figure 3.6.7. Cumulative elasticity effect by for egg, juvenile and adults stages of Kentucky Lake, Tennessee population with 20 age groups.
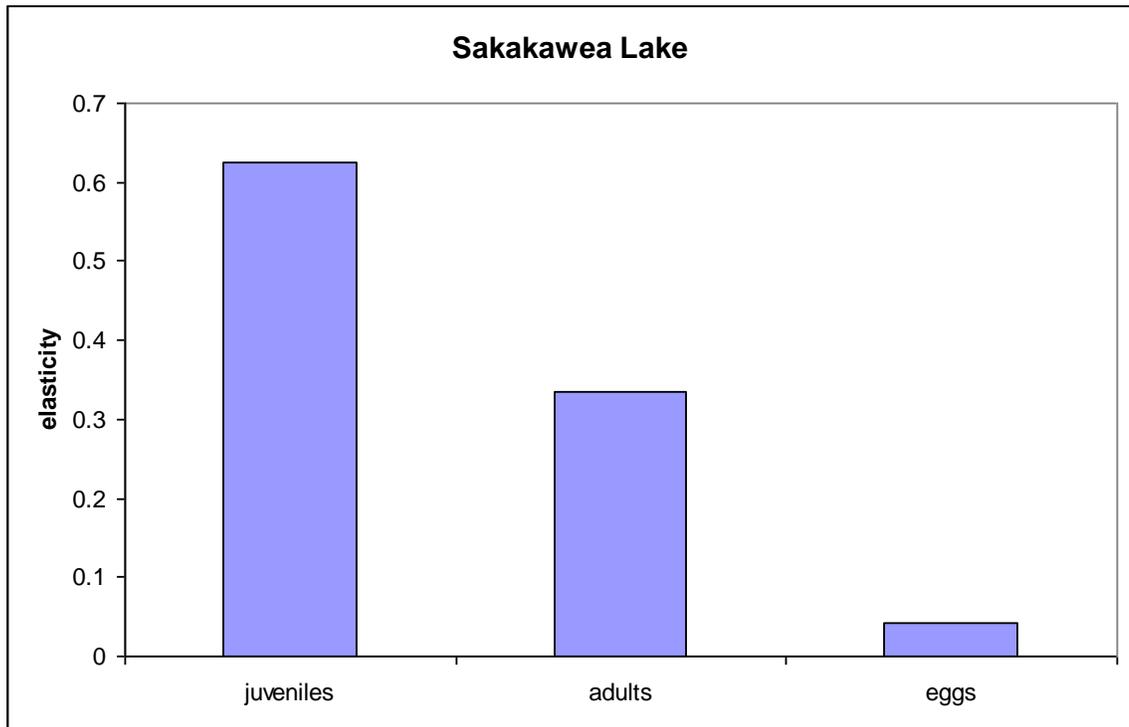

Figure 3.6.8. Cumulative elasticity effect by for egg, juvenile and adults stages of Sakakawea Lake, North Dakota population with 60 age groups.
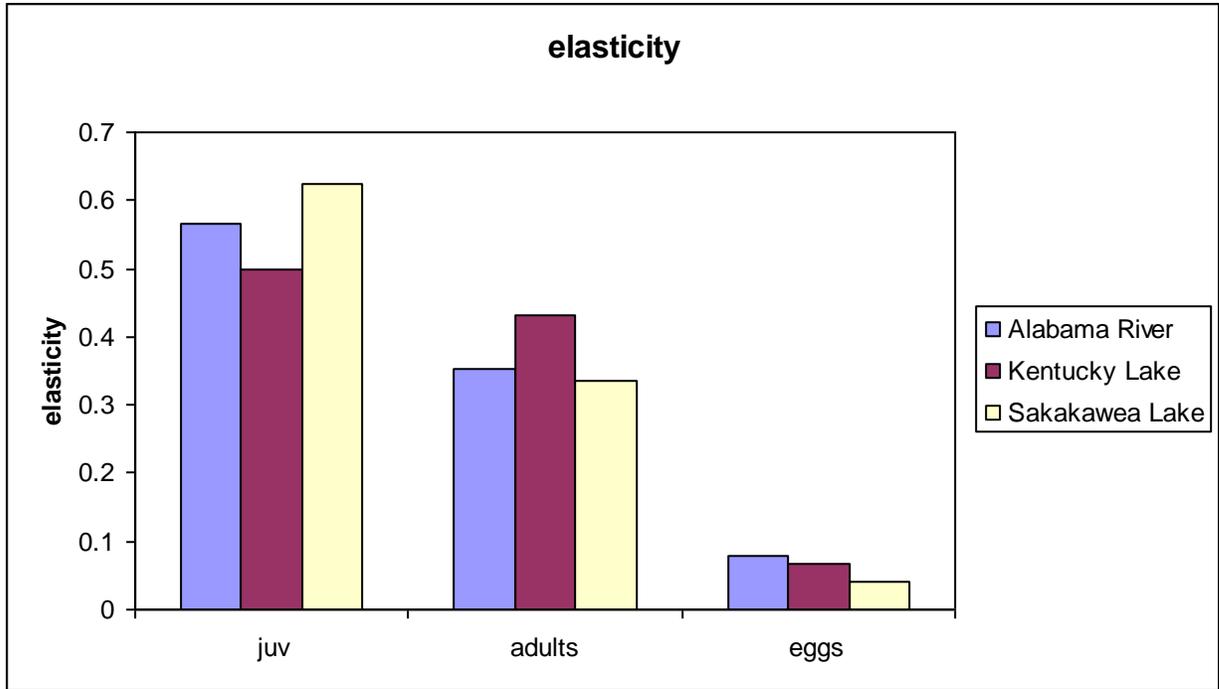
Figure 3.6.9. Cumulative elasticity comparison among analyzed stocks by stages.
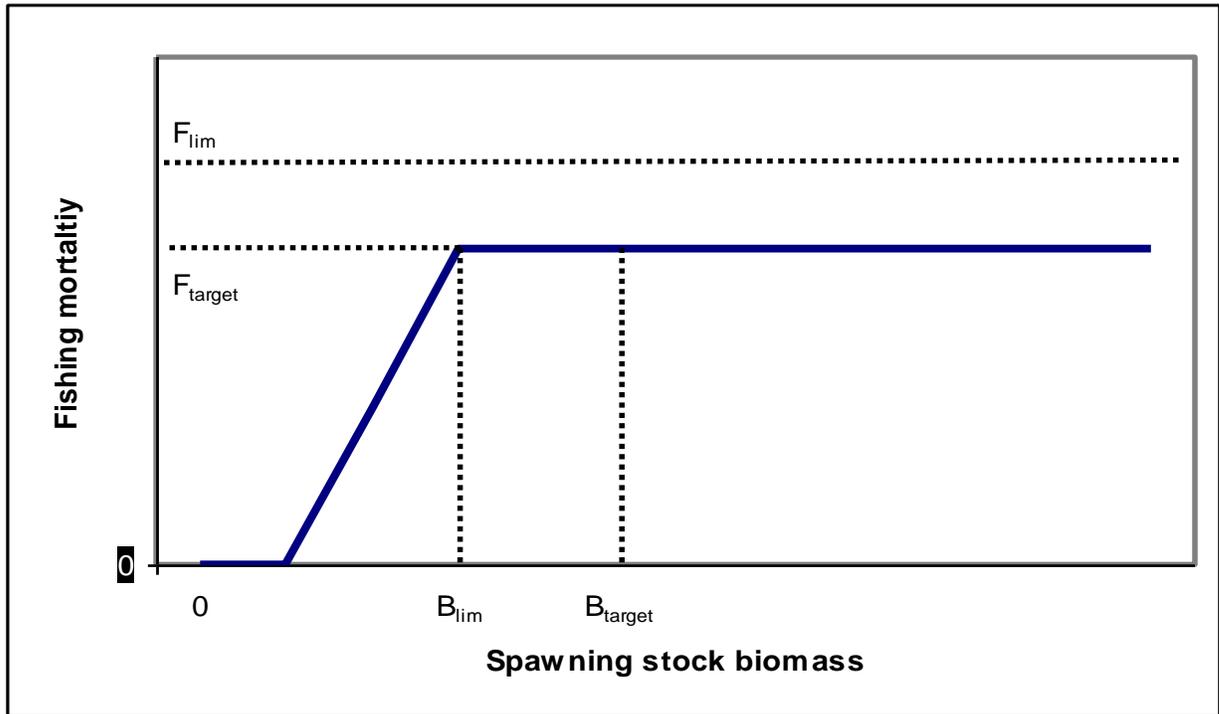
Figure 3.7.1. Harvest control rule. B_{lim} is biomass threshold that represents the lower limit for spawning stock biomass. B_{target} is the desirable level of spawning stock biomass management should aim for. F target is fishing mortality that on average should be maintained, F_{lim} is maximum limit of

fishing mortality that should not be exceeded. When biomass declines below B_{lim}, fishing mortality should be reduced according to the control rule (blue line).