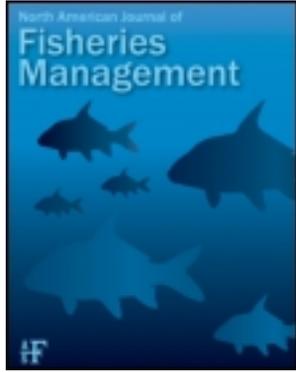


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Predicting Paddlefish Roe Yields Using an Extension of the Beverton-Holt Equilibrium Yield-per-Recruit Model

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ARTICLE

Predicting Paddlefish Roe Yields Using an Extension of the Beverton–Holt Equilibrium Yield-per-Recruit Model

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Abstract

Equilibrium yield models predict the total biomass removed from an exploited stock; however, traditional yield models must be modified to simulate roe yields because a linear relationship between age (or length) and mature ovary weight does not typically exist. We extended the traditional Beverton–Holt equilibrium yield model to predict roe yields of Paddlefish *Polyodon spathula* in Kentucky Lake, Tennessee–Kentucky, as a function of varying conditional fishing mortality rates (10–70%), conditional natural mortality rates (cm ; 9% and 18%), and four minimum size limits ranging from 864 to 1,016 mm eye-to-fork length. These results were then compared to a biomass-based yield assessment. Analysis of roe yields indicated the potential for growth overfishing at lower exploitation rates and smaller minimum length limits than were suggested by the biomass-based assessment. Patterns of biomass and roe yields in relation to exploitation rates were similar regardless of the simulated value of cm , thus indicating that the results were insensitive to changes in cm . Our results also suggested that higher minimum length limits would increase roe yield and reduce the potential for growth overfishing and recruitment overfishing at the simulated cm values. Biomass-based equilibrium yield assessments are commonly used to assess the effects of harvest on other caviar-based fisheries; however, our analysis demonstrates that such assessments likely underestimate the probability and severity of growth overfishing when roe is targeted. Therefore, equilibrium roe yield-per-recruit models should also be considered to guide the management process for caviar-producing fish species.

Biologists have modeled fishery yields for decades, and the advent of software such as the Fisheries Analysis and Modeling Simulator (FAMS, previously known as FAST; Slipke and Maceina 2010) has encouraged the use of yield models in freshwater fisheries. Data requirements for yield models (e.g., the Beverton–Holt equilibrium yield model; Beverton and Holt 1957) are straightforward (although perhaps difficult to obtain) and include estimates of fishing mortality and natural mortality, length-at-age data, and weight-at-length data. Predicted yield is

typically expressed in terms of biomass, or the weight of fish that are removed from an exploited stock.

Traditional yield models are not applicable when a fishery targets roe for caviar because of interactions among ovary weight, sexual maturity, age, and length and because the harvest of sexually immature fish does not contribute to roe yields. For example, the relationship between eye-to-fork length (EFL) and ovary weight for Paddlefish *Polyodon spathula* differs markedly between mature and immature females (e.g., Scholten

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and Bettoli 2005). Specifically, a Paddlefish of any length or maturity status has a body weight; however, only mature female Paddlefish have ovarian weights that contribute to roe harvests. Additionally, ovary weights of mature Paddlefish will vary by more than an order of magnitude among larger individuals (Jennings 2000), whereas the total body weight of similar-length mature fish is much less variable over a wide size range. Variation in ovary weight at a specified length or age is due in part to the nonlinear (e.g., sigmoidal) pattern of population sexual maturation, resulting in only the largest age-classes and size-classes reaching 100% maturity. Therefore, roe yield of an exploited population is the result of interactions among ovary weight, sexual maturity, and size, which cannot be described as a simple linear function of biomass yield.

In Tennessee and elsewhere, interest in modeling the roe yields of Paddlefish is high for several reasons. First, commercial fisheries for Paddlefish are usually managed to maximize roe yields rather than flesh yields (Bettoli et al. 2007; Quinn 2009; Scholten 2009). Second, Paddlefish are enduring increased harvest pressure with the decline of Eurasian sturgeon stocks (e.g., Beluga *Huso huso*), and there are widespread concerns that Paddlefish stocks are being overfished in some locales (Quinn 2009). Scholten and Bettoli (2005) modeled Paddlefish yield per recruit in Kentucky Lake, Tennessee–Kentucky, and concluded that this stock was experiencing modest growth overfishing (i.e., fish were being harvested at an average size less than the size that maximizes yield) in terms of biomass. The implication of this result was that the stock also likely suffered from growth overfishing in terms of roe yield, but the traditional Beverton–Holt yield-per-recruit model could not be used to directly assess the degree to which roe yields might be improved if recruitment to the fishery was delayed by raising the minimum size limits. Another reason for investigating whether roe yields could be increased by reducing fishing mortality is the high roe prices received by commercial fishers in Tennessee during recent years (i.e., US\$165–220 per kilogram wholesale between 2008 and 2011; E. Ganus, Tennessee Wildlife Resources Agency, personal communication). The Paddlefish caviar trade represents an important source of revenue in small river communities of rural Tennessee, and maximizing economic value is important to politicians and to the fishing industry. Finally, management of Paddlefish roe fisheries in Tennessee has become a contentious issue in recent years. For instance, a bill was introduced in 2011 by the Tennessee legislature to set seasons and length limits on Paddlefish, and a lawsuit claiming mismanagement of Paddlefish in Tennessee was filed by a fishing industry trade group against the Tennessee Wildlife Resources Commission.

For species that are commercially exploited for caviar, the modeling of yields based on total biomass is a common practice (e.g., Rieman and Beamesderfer 1990; Quist et al. 2002; Colombo et al. 2007); however, we are unaware of any previous attempt to simulate the effects of fishing mortality and harvest regulations on roe yields. In this study, we modified the traditional Beverton–Holt equilibrium yield model to

predict biomass yield accounting for sex-dependent growth and roe yield under varying exploitation rates, natural mortality rates, and minimum size limits for the Paddlefish fishery in Kentucky Lake, which was previously analyzed by Scholten and Bettoli (2005). We then used the model to compare equilibrium biomass and roe yields and to assess the potential for growth overfishing in terms of roe yields. Finally, we used the roe yield model to calculate spawning potential ratios (SPRs) and to assess the potential for recruitment overfishing in the Kentucky Lake Paddlefish fishery.

METHODS

Study Area

Kentucky Lake is a mainstream impoundment of the Tennessee River, located in western Tennessee and Kentucky (37.01°N, 88.27°W). Impounded in 1944 by Kentucky Dam at Tennessee River kilometer 35, this 296-km-long reservoir is a eutrophic impoundment that covers 64,870 ha at full pool. Water discharged from Pickwick Dam (the upstream boundary of the lake at Tennessee River kilometer 331) flows north through Kentucky Lake. Tennessee was one of six states that allowed the commercial harvest of Paddlefish for their roe beginning in 2006 (Bettoli et al. 2009). Those states currently remain open to commercial harvest, and an additional fishery has opened in Mississippi. The current minimum length limit for Paddlefish harvested in the Kentucky Lake system is 914 mm EFL. Kentucky Lake has traditionally provided most of the Tennessee Paddlefish roe destined for domestic and international markets, although in recent years export permits have been denied by the U.S. Fish and Wildlife Service (USFWS) Office of Scientific Authority over concerns that the stock was being overfished (M. Maltese, USFWS, personal communication).

Data Collection

A complete description of field collections and sample processing was provided by Scholten and Bettoli (2005). In summary, most Paddlefish were collected between September 2003 and May 2004 by using horizontal experimental gill nets. The mesh size in the six panels of each net ranged from 89- to 203-mm bar measure. Additional data from Paddlefish captured by commercial fishers were obtained from 15 November 2003 to 23 April 2004. The EFL (mm), weight (nearest 0.25 kg), sex, and maturity status were recorded for each Paddlefish. Sex and maturity were determined by examining the gonads. Females with partially developed or immature ova (usually white or mottled) were categorized as immature. Females were classified as mature if their ovaries contained large (2–3-mm diameter), dark eggs (Bronte and Johnson 1985). Ovaries were excised from all females and were weighed to the nearest 0.1 g. Dentary bones of at least five Paddlefish per 25-mm EFL group were removed for use in age estimation. Ages were then assigned to unaged fish by using an age–length key. Fish collected during these efforts were used to parameterize the yield models detailed below.

Yield Model Construction

Flesh and roe yields were calculated by extending the basic yield model, where yield (either biomass or roe) is calculated by multiplying the number and average weight of fish material captured (Everhart and Youngs 1953; Beverton and Holt 1957; Ricker 1975; Die et al. 1988). Total yield can be calculated by integrating the sum of the sex-specific product of the number of fish captured and mean weight from the age (t) at which a fish of sex i is recruited to the fishery to the maximum fish age. Formally, total yield (accounting for sex-specific growth) is calculated by evaluating the integral

$$\text{Yield} = \sum_{i=1}^2 \int_{t_{r,i}}^{t_{\lambda}} [C(t)_i W(t)_i] dt, \quad (1)$$

where t_{λ} is maximum fish age, $C(t)_i$ is a function predicting the age-specific number of fish of sex i that were caught, $W(t)_i$ is an age-dependent function predicting the mean weight of harvested material (i.e., biomass or roe) for fish of sex i , and dt is the change in age. The yield equation requires two sex-specific functions relating the number (i.e., catch at age) and weight (i.e., weight at age) of fish at age t (Die et al. 1988).

Catch at age.—Our model assumes that commercial harvest of Paddlefish does not discriminate between maturity stage or sex. The only reliable method for determining sex and sexual maturity (for males and immature females) is to dissect captured fish that are greater than the minimum length limit. Therefore, the sex-specific function relating age-specific catch is the same regardless of whether biomass or roe yield is of interest; the number of captured age- t fish of sex i was calculated as

$$C(t)_i = F \cdot R_i \cdot e^{-(M \cdot t_{r,i})} \cdot e^{-(M+F)(t-t_{r,i})}, \quad (2)$$

where F is the instantaneous fishing mortality rate, R_i is the number of fish of sex i that recruited to the fishery, M is the instantaneous natural mortality rate, $t_{r,i}$ is the sex-specific age at recruitment to the fishery for fish of sex i , and t is fish age (Everhart and Youngs 1953; Ricker 1975). This equation is a modification of the traditional function used to predict catch at age in the Beverton–Holt equilibrium yield model (Beverton and Holt 1957) and accounts for sex-specific yield differences.

Eye-to-fork length at age.—A sex-specific length-at-age function is a key component required to calculate total biomass or roe yield while accounting for differential growth between males and females. In particular, weight (whole fish or roe) is more accurately predicted as a function of length. However, the basic yield equation predicts total yield as a function of age; therefore, length (EFL in this case) was converted to age for integration. This was accomplished by assuming that sex-specific von Bertalanffy growth functions (VBGFs) adequately describe fish length (EFL) as a function of age and sex:

$$\text{EFL}(t)_i = \text{EFL}_{\infty,i} [1 - e^{-k_i(t-t_{0,i})}]. \quad (3)$$

Specifically, the above VBGF equation predicts length based on age, where EFL is in millimeters, $\text{EFL}_{\infty,i}$ is the asymptotic EFL, k_i is the Brody growth coefficient, t is age, $t_{0,i}$ is the theoretical age at a length of zero, and i indexes sex (Ricker 1975).

Weight-at-Age Functions

Fish weight at age.—Sex-specific parameter estimates for the EFL–weight relationship were estimated by using field data. Fish weight at length was estimated by fitting the standard equation that describes the allometric scaling of weight with length (i.e., $\text{weight} = aL^b$, where L = length) and then allowing the a - and b -parameters to vary for males and females. Fish weight at EFL was then calculated as

$$W_{\text{fish}}(t)_i = a_i \cdot \text{EFL}(t)_i^{b_i}, \quad (4)$$

where a_i and b_i are sex-specific parameters of the EFL–weight relationship, and $\text{EFL}(t)_i$ is the sex-specific VBGF.

Roe weight-at-age.—Calculation of roe weight at age required a roe weight-at-age function (for females only) that accounted for age-dependent sexual maturity and ovary weight as

$$W_{\text{roe}}(t) = [\text{mat}(t)] [\text{ow}(t)], \quad (5)$$

where $\text{mat}(t)$ and $\text{ow}(t)$ are age-dependent functions predicting the mature fraction and the ovary weight, respectively, of female Paddlefish. Paddlefish females ($n = 357$) collected from Kentucky Lake were used to develop the predictive relationships for maturity and ovary weight (detailed below).

Maturity at eye-to-fork length.—Maturity was associated with EFL, and a small fraction of female Paddlefish became sexually mature at age 8 (Table 1; Figure 1). A general linear model assuming a binomial distribution was used to predict maturity as a function of EFL (Gelman and Hill 2007). Specifically, the general linear model predicted the proportion of sexually mature females as a function of EFL:

$$\text{mat}(\text{EFL}) = [e^{(\beta_0 + \beta_1 \cdot \text{EFL})}] / [1 + e^{(\beta_0 + \beta_1 \cdot \text{EFL})}]. \quad (6)$$

A chi-square test was used to assess model goodness of fit, where failure to reject the null hypothesis (i.e., $P > 0.05$) indicated an adequate fit to the data.

Ovary weight at eye-to-fork length.—Ovary weight was modeled as a function of sexual maturity status and EFL. Specifically, mean ovary weight at EFL accounting for maturity status was predicted by fitting the equation:

$$\log_e(\text{OW}) = \beta_0 + \beta_1 \cdot \text{Mature} + \beta_2 \cdot \log_e(\text{EFL}) + \beta_3 \cdot [\log_e(\text{EFL}) \cdot \text{Mature}], \quad (7)$$

where OW is ovary weight, β_0 is the intercept, β_1 is the effect of whether a female is mature, β_2 accounts for the effect of EFL on ovary weight, and β_3 accounts for the interaction of whether

TABLE 1. Maturity (%), mean eye-to-fork length (EFL; mm), mean body weight (kg), and mature ovary weight (kg) for each age-class of female Paddlefish collected from Kentucky Lake, Kentucky–Tennessee, by use of commercial and experimental gill nets, 2003–2004.

Age	Number	Percent mature	EFL		Weight		Mature ovary weight	
			Mean	SE	Mean	SE	Mean	SE
2	3	0	510	7.5	1.50	0.06	0	
3	4	0	552	17.4	2.27	0.11	0	
4	14	0	661	11.9	4.76	0.39	0	
5	16	0	731	14.9	6.12	0.4	0	
6	58	0	821	6.4	9.17	0.27	0	
7	65	0	862	7.8	10.99	0.38	0	
8	99	16	932	6.2	14.27	0.33	2.26	0.07
9	49	51	969	7.1	15.67	0.48	2.09	0.04
10	38	92	1,006	8.6	17.55	0.65	2.34	0.02
11	8	88	1,045	21.1	20.04	1.58	2.17	0.24
12	1	100	1,020		16.50		2.79	

a female is mature on the estimate of β_2 . The model used to estimate ovary weight for sexually mature fish was simplified to account for interactions and was used in subsequent yield analysis.

Full equilibrium yield models.—Fish and roe yields were calculated by substituting catch-at-age and roe weight-at-age functions into the base yield equation (equation 1) as

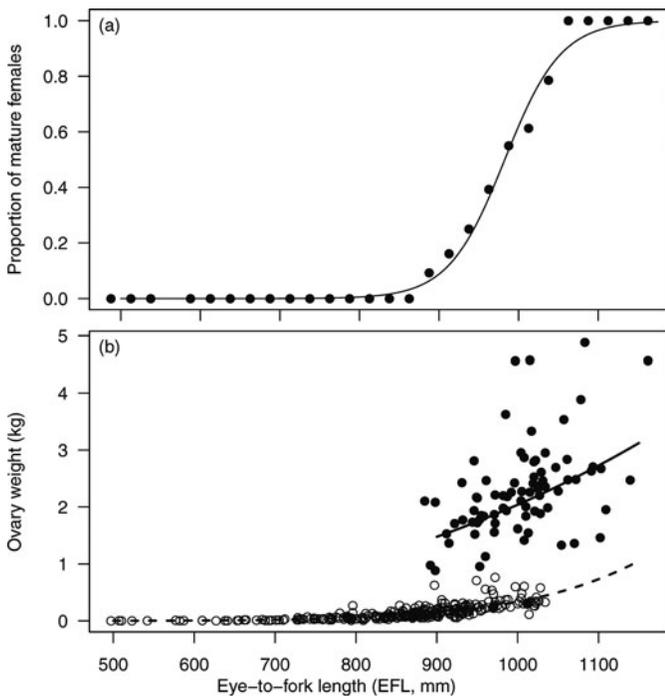


FIGURE 1. Plot of (a) maturity or (b) ovary weight in relation to eye-to-fork length (EFL) for female Paddlefish collected from Kentucky Lake, Kentucky–Tennessee, in 2003–2004. In panel a, points are the proportion of mature females per 25-mm length-group, and the line represents a logistic function fitted to the observed data. In panel b, points represent ovary weights from immature (open circles) or mature (shaded circles) females, and the solid line represents the best-fit model for predicting ovary weight from EFL for immature (dashed line) or mature (solid line) females.

$$Y_{fish} = \sum_{i=1}^2 \int_{t_{r,i}}^{t_x} \left(F_{t,i} \cdot R_i \cdot e^{-(M \cdot t_{r,i})} \cdot e^{-(M+F)(t-t_{r,i})} \cdot a_i \{EFL_{\infty,i} [1 - e^{-k_i(t-t_{0,i})}] \}^{b_i} \right) dt, \quad (8)$$

and

$$Y_{roe} = \int_{t_{r,1}}^{t_x} \left(F \cdot R_1 \cdot e^{-(M \cdot t_{r,1})} \cdot e^{-(M+F)(t-t_{r,1})} \cdot \frac{e^{\{\beta_0 + \beta_1 \cdot EFL_{\infty,1} [1 - e^{-k_1(t-t_{0,1})}]\}}}{1 + e^{\{\beta_0 + \beta_1 \cdot EFL_{\infty,1} [1 - e^{-k_1(t-t_{0,1})}]\}}} \cdot a_1 \{EFL_{\infty,1} [1 - e^{-k_1(t-t_{0,1})}] \}^{b_1} \right) dt, \quad (9)$$

where the parameters and variables are as previously described. Full models incorporating the parameter estimates and variables used in subsequent equilibrium yield analysis are presented in Tables 2 and 3.

Simulation of Equilibrium Yield

Four minimum EFL limits were used to simulate flesh and roe yields: 864 mm (historic [pre-2005] limit), 914 mm (current limit), 965 mm, and 1,014 mm EFL. Minimum length limits were converted to age by solving the VBGF, and the ages were used as values of $t_{r,i}$ for sex i given the sex-specific VBGF. A maximum age (t_x) of 21 years was used in the previous analysis of Kentucky Lake Paddlefish (Scholten and Bettoli 2005). To maintain consistency with previous analyses of North American

TABLE 2. Parameterized versions of the in-text equations required to simulate biomass and roe yield for the Paddlefish population in Kentucky Lake. See Table 3 for definitions of parameters and variables.

Equation number	Formula
Females (<i>i</i> = 1)	
3	$EFL(t) = 1,279[1 - e^{-0.14(t+1.29)}]$
4	$W_{fish}(t) = e^{-20.1} \cdot EFL(t)^{3.327}$
6	$mat(EFL) = [e^{(-27.78+0.028 \cdot EFL)}] / [1 + e^{(-27.78+0.028 \cdot EFL)}]$
7	$\log_e(OW) = -50.7 + [37.2 \cdot Mature] + [3.0529 \cdot \log_e(EFL)] + \{-5.1 \cdot [\log_e(EFL) \cdot Mature]\}$
Males (<i>i</i> = 2)	
3	$EFL(t) = 898[1 - e^{-0.38(t+0.33)}]$
4	$W_{fish}(t) = e^{-14.5} \cdot EFL(t)^{2.472}$
Equilibrium yield equations	
8	$Y_{fish} = \int_{t_r,1}^{t_\lambda} \{F_{t,1} \cdot R_1 \cdot e^{-(M \cdot 8.3)} \cdot e^{-(M+F_{t,1})(t-8.3)} \cdot e^{-20.1} \cdot 1,279[1 - e^{-0.14(t+1.29)}]^{3.327}\} dt$ $+ \int_{t_r,2}^{t_\lambda} \{F_{t,2} \cdot R_2 \cdot e^{-(M \cdot 6.7)} \cdot e^{-(M+F_{t,2})(t-6.7)} \cdot e^{-14.5} \cdot 898[1 - e^{-0.38(t+0.33)}]^{2.472}\} dt$
9	$Y_{roe} = \int_{t_r,1}^{t_\lambda} [F \cdot R_1 \cdot e^{-(M \cdot t_{r,1})} \cdot e^{-(M+F)(t-t_{r,1})} \cdot \frac{e^{(-27.78+0.028(1,279[1 - e^{-0.14(t+1.29)}]^{3.0529}))}}{1 + e^{(-27.78+0.028(1,279[1 - e^{-0.14(t+1.29)}]^{3.0529}))}} \cdot 0.0000014\{1,279[1 - e^{-0.14(t+1.29)}]^{3.0529}\}] dt$

sturgeon species, knife-edge recruitment of Paddlefish to the fishery was assumed.

Paddlefish natural mortality was less than 9% in a subimpoundment on the Cumberland River, Tennessee, where fishing was prohibited (Boone and Timmons 1995); furthermore, Timmons and Hughbanks (2000) suggested that natural mortality was low (~8%) for Paddlefish in Kentucky Lake. Previous yield analysis of the Kentucky Lake population by Scholten and Bettoli (2005) used a conditional natural mortality rate (*cm*) of 8%. However, *cm* should be slightly higher than natural mortality if any fishing is occurring; therefore, a *cm* of 9% was used in this analysis. Additional simulations were evaluated for a *cm* of 18% to assess the sensitivity of results to uncertainty

in natural mortality rates. This higher *cm* falls within the range (13–20%) we estimated by using multiple natural mortality estimators (Hoening 1983; Peterson and Wroblewski 1984; Jensen 1996; Quinn and Deriso 1999) and an assumed maximum age of 21, and it represents a probable maximum natural mortality rate given the lowest observed total mortality rate from a previous study of this population (22%; Timmons and Hughbanks 2000). Natural mortality rates were assumed to be the same for male and female Paddlefish. Values of *cm* were converted to *M*. The current analysis assumed 1,000 age-0 recruits (*R*) to the population, which is a common assumption in equilibrium yield models and was used in the previous analysis by Scholten and Bettoli (2005). The analysis by Scholten and Bettoli (2005) used a sex ratio of 1.0:1.5 (male : female); therefore, the female fraction of age-0 fish that recruited to the population was 0.6, while the male fraction was 0.4 (i.e., *R*₁ = 600 female recruits; *R*₂ = 400 male recruits). Overall results did not differ for varying sex ratios, and therefore we report results for the 1.0:1.5 ratio.

Yields were simulated for conditional fishing mortalities (*cf*) increasing from 0.1 to 0.7. Values of *cf* were first converted to *F*, and annual survival was calculated for each combination of *F* and *M*. Exploitation rates (*u*) were then calculated and used in graphical analysis of yield to maintain consistency with previous yield modeling of Paddlefish in Kentucky Lake. Growth overfishing was illustrated in graphical analysis as a dome-shaped relationship between yield and exploitation.

Solving the Yield Model Equations

Equation (8) can be solved by using the Jones (1957) method, whereas a straightforward analytical or approximate solution to equation (9) is unavailable, thus requiring numerical integration. Therefore, in this analysis, total equilibrium yield (biomass or roe) was calculated by numerically integrating equations (8) and

TABLE 3. Definitions of parameters and variables used in Table 2.

Variable or parameter	Definition and units
<i>t</i>	Age (years)
EFL(<i>t</i>)	Eye-to-fork length (mm) at age <i>t</i>
<i>F</i>	Instantaneous fishing mortality (year ⁻¹)
<i>R</i>	Recruits (number of fish)
<i>M</i>	Instantaneous natural mortality (year ⁻¹)
<i>t_r</i>	Age (years) at recruitment to the fishery
<i>t_λ</i>	Maximum age (years)
<i>Mature</i>	Variable indexing maturation (0 = immature; 1 = mature)
<i>W_{fish}(t)</i>	Fish weight at age (kg)
<i>mat</i> (EFL)	Mature fraction at EFL (unitless)
OW	Ovary weight (kg)
<i>Y_{fish}</i>	Biomass yield (kg)
<i>Y_{roe}</i>	Roe yield (kg)

(9) from $t_{r,i}$ to t_λ using the integrate function in R software (R Development Core Team 2010) for all combinations of F and M .

Spawning Potential Ratio

Spawning potential ratios based on fecundity are frequently used in combination with yield modeling to evaluate the potential for recruitment overfishing. Given that roe yield of gravid females was being modeled, the amount of mature ovary biomass left after harvest (i.e., potential spawning biomass) was used to calculate the SPR. Specifically, spawning stock potential (SSP) was calculated by simply modifying equation (9) to calculate the amount of mature ovary biomass at age t via removal of the first F -parameter as

$$SSP = \int_{t_{r,1}}^{t_\lambda} \left\{ R_1 \cdot e^{-(M \cdot t_{r,1})} \cdot e^{-[(M+F)(t-t_{r,1})]} \cdot \frac{e^{[\beta_0 + \beta_1 \cdot EFL(t)_1]}}{e^{[\beta_0 + \beta_1 \cdot EFL(t)_1]} + 1} \cdot [a_{ovary} \cdot EFL(t)_1^{b_{ovary}}] \right\} dt. \quad (10)$$

Equation (10) is a continuous analog to the discrete approximation used to calculate SSP as provided by Goodyear (1993). The SPR was then calculated as

$$SPR = SSP_{fished} / SSP_{unfished}, \quad (11)$$

where SSP_{fished} and $SSP_{unfished}$ are the spawning stock potentials for $F > 0$ and $F = 0$, respectively. The SPRs resulting from equation (11) were similar to values calculated in FAMS by using the method of Goodyear (1993). All statistical and simulation analyses were conducted in R (R Development Core Team 2010). Code to reproduce the yield and SPR analyses is available upon request from the corresponding author.

RESULTS

Simulated Yields

Biomass yield.—Biomass (i.e., flesh) yield per 1,000 recruits varied among minimum length limits and between the two cm levels (Figure 2). In general, biomass yield increased with u for all length limits and both cm values, with maximum yields occurring at or near the largest modeled values of u ; thus, there was little evidence for growth overfishing (Table 4; Figure 2). Biomass yield was maximized at a high exploitation level ($u \sim 61\%$) for the 864-mm minimum length limit and the cm of 9%. Yield increased across the range of simulated u -values for the 864-mm minimum length limit when cm was 18%. Regardless of the cm level, yield increased with increasing u for the 914-, 965-, and 1,016-mm minimum length limits. A decrease in biomass yield was apparent when the minimum length limit increased from the 864-mm historic limit; this result was due to differences in growth and the underlying sex-specific VBGF parameters. Specifically, the EFL_∞ parameter for the male VBGF was 894 mm; therefore, minimum length limits that exceed this

TABLE 4. Exploitation rates (u ; %) at which simulated biomass and roe yields were maximized and at which the spawning potential ratio (SPR) was 30% under varying conditional natural mortality rates (cm) and minimum length limits evaluated for the Paddlefish population in Kentucky Lake. The SPR is the ratio of mature ovary biomass in an exploited population and an unexploited population.

cm (%)	Minimum length limit (mm)	u		
		Biomass _{max}	Roe _{max}	SPR ₃₀
9	864	61	14	15
	914	70	17	17
	965	70	24	22
	1,016	70	37	31
18	864	70	17	17
	914	70	23	21
	965	70	36	29
	1,016	70	70	50

EFL will protect male Paddlefish from harvest and will reduce overall biomass yield.

Roe yields.—Roe yields per 1,000 recruits varied more dramatically than biomass yields among minimum length limits at both of the simulated cm levels (Figure 2). Roe yield increased to a maximum with increasing u , followed by a decrease in yield for all minimum length limits when cm was 9%. Simulated roe yields exhibited similar patterns when cm was 18%, with yields increasing to a maximum at intermediate values of u , followed by yield decreases for all but the largest length limit (Table 4). Specifically, roe yields were maximized at u levels ranging from 14% to 27% for a cm of 9% and at u levels from 17% to 70% for a cm of 18%. Growth overfishing in terms of roe yields was apparent under both of the cm scenarios at the historic and current minimum length limits when u exceeded modest levels (i.e., 14–37% for $cm = 9\%$; 17–36% for $cm = 18\%$).

Spawning Potential Ratio

The SPR varied among the four minimum length limits and between the two levels of cm (Figure 2). Patterns of decreasing SPR with increasing u were similar between the cm levels; however, decreases in SPR were more rapid when cm was equal to 9%. A narrow range of u -values maintained SPR above 0.2–0.3, which was recommended by Goodyear (1993) as an SPR threshold for most fish populations and was previously used in the analysis by Scholten and Bettoli (2005). Results indicated the potential for recruitment overfishing when low levels of u were exceeded, especially with liberal minimum length limits, regardless of the simulated cm level (Table 4). In particular, the u -value that produced an SPR of 30% (SPR₃₀) increased from 15% to 31% with increasing minimum length limit for a cm of 9%. Exploitation rates that generated SPR₃₀ were higher for a cm value of 18%, increasing from 17% to 50% with increasing minimum length limit. When viewed in conjunction with

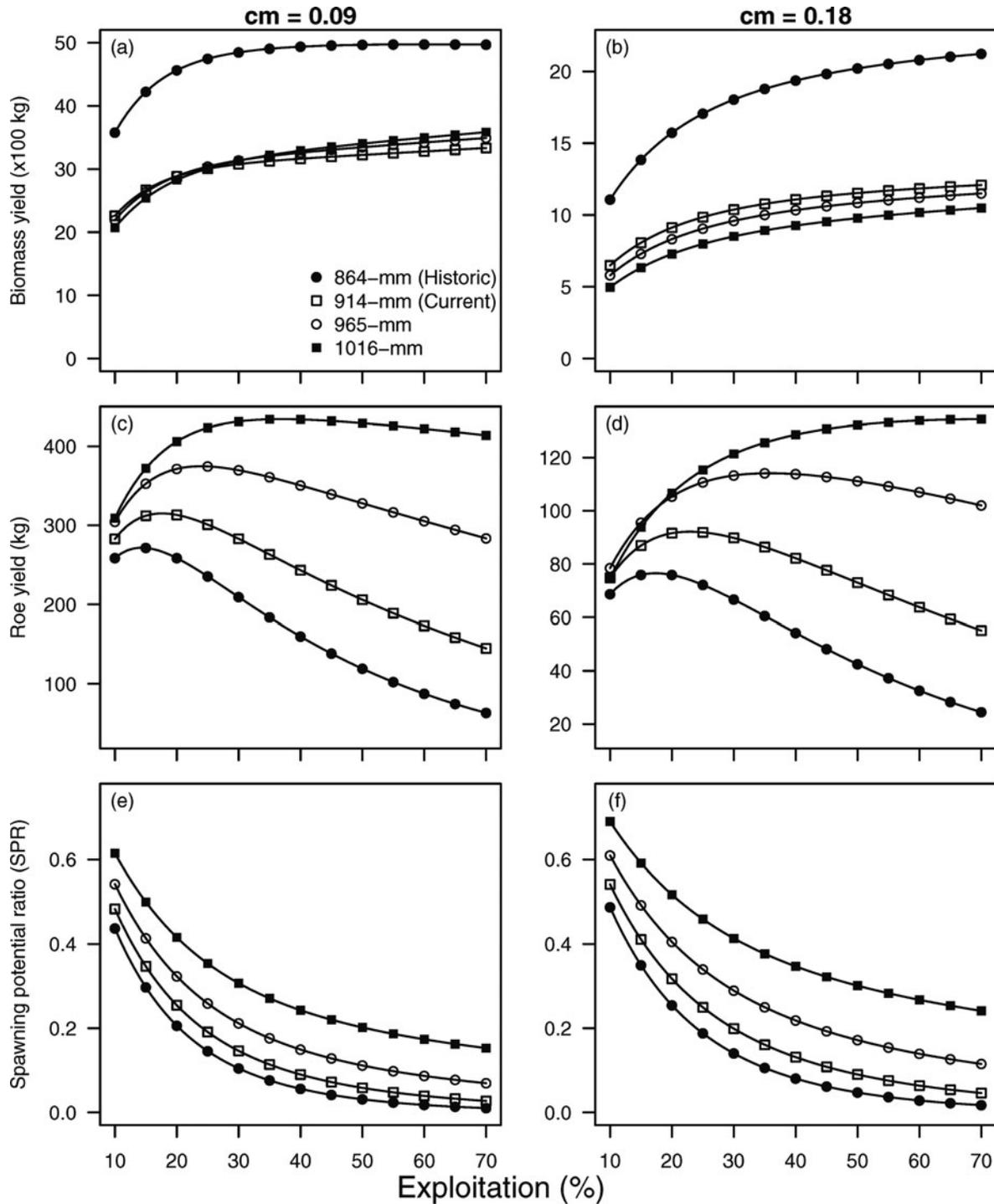


FIGURE 2. Predicted (a), (b) Paddlefish biomass yields; (c), (d) roe yields; and (e), (f) spawning potential ratios (SPRs) for two levels of conditional mortality (cm) and four minimum length limits (mm) in Kentucky Lake. Yields were predicted per 1,000 recruits.

roe yield simulations, the potential for growth overfishing (in terms of roe yield) and for recruitment overfishing was minimized with higher minimum length limits, regardless of the cm level.

DISCUSSION

This study extended the Beverton–Holt equilibrium yield model to evaluate biomass yields given sex-dependent growth as well as roe yield, which is increasingly important considering

the number of previous studies that have used biomass-based equilibrium yield models in assessments of caviar-producing fishes. Biomass-based yield assessments are currently used to assess fishing impacts on caviar-producing fish stocks because of the perceived risks of overfishing due to increased caviar demand (e.g., Quist et al. 2002; Kennedy and Sutton 2007; Koch et al. 2009; Leone et al. 2012). Generally, these types of studies conclude that growth overfishing occurs at low minimum length limits, providing justification for higher minimum length limits. For example, Koch et al. (2009) showed that a 685-mm length limit was needed to prevent growth overfishing for several populations of Shovelnose Sturgeon *Scaphirhynchus platyrhynchus* in the Upper Mississippi River. A recent study of Paddlefish in Arkansas suggested that growth overfishing may occur with an 833-mm length limit (Leone et al. 2012). However, the results of the present study indicate that biomass-based yield assessments are likely to underestimate the potential for and the severity of growth overfishing when roe is being targeted, even if sex-dependent growth is accounted for in the biomass yield model.

Discrepancies between the effect of varying u and minimum length limits on biomass and roe yields reflect the interactions of maturity, sex ratio, and ovary weight. Roe yields increased with minimum length limit for both of the cm levels simulated. This result reflects the effect of larger minimum length limits delaying recruitment of younger, immature fish to the fishery, thereby allowing them to become larger and increasing their likelihood of being sexually mature at harvest. Consequently, roe yield increases, as more harvested females are likely to be gravid with larger ovaries.

Given the declines in European stocks of caviar-producing acipenseriform fishes and the high market value for roe (Birstein 1993), equilibrium yield-per-recruit analyses will likely continue to be an important tool for assessing and managing fisheries associated with caviar-producing species. The present analysis provides a method for evaluating equilibrium roe yield given a stock-specific maturation schedule and ovary weights. Females in the Kentucky Lake Paddlefish population are believed to spawn every year once they reach sexual maturity (Scholten and Bettoli 2005). However, the spawning of females every other year (or up to every 3 years) has been noted in other Paddlefish and sturgeon populations (Quist et al. 2002). The effect of variable spawning frequency on the generalization of our methods to other caviar-producing species is uncertain; however, this has not precluded SPR analyses (i.e., which account for the number of females spawning annually by age-class) from being used for those populations (e.g., Quist et al. 2002; Koch et al. 2009). Given that the models for roe yield and SPR are related, our approach to modeling roe yields can likely be generalized to fishes with variable spawning frequency and is at least better than biomass-based yield assessments; however, this topic requires further research.

Identification and implementation of harvest strategies that reduce the likelihood of both growth overfishing and recruitment overfishing would help to ensure a sustainable fishery for

Paddlefish roe. However, it is difficult to perfectly manage the fishery, especially if fishing effort, harvest, or realized u is associated with uncontrollable environmental factors (i.e., partial harvest control). Specifically, Scholten and Bettoli (2005) observed a threefold increase in the number of harvested Paddlefish with increases in the number of fishable days on Kentucky Lake (i.e., days with mean Pickwick Dam discharge $< 850 \text{ m}^3/\text{s}$). Pickwick Dam is operated to provide flood control, navigation, and power production and cannot be operated to manage harvest by limiting fishable days; therefore, regulations that are robust to variation in u and that can maximize yields are desirable. For example, relative to the other minimum length limits evaluated in our analysis, the largest length limit (1,016 mm) provided the most protection from growth overfishing and recruitment overfishing while also maximizing roe yield across a broad range of u -values and cm levels.

Paddlefish fisheries target roe because of lucrative roe prices that greatly exceed the value of flesh. However, Paddlefish flesh can also be sold to provide additional revenue (Scholten and Bettoli 2005). Therefore, analysis of both flesh and roe yields may be important for management of the fishery to minimize economic consequences, which is of concern in the rural areas where commercial fishers reside. Specifically, the effect of varying length limits and u on the potential economic yield of the Kentucky Lake Paddlefish fishery could be evaluated as the sum of the estimated economic yields of roe and flesh. For example, assuming market prices of \$220 per kilogram for roe and \$1.10 per kilogram for flesh, the equilibrium yields presented in Figure 2 can be combined into a single monetary value (Figure 3). For the Kentucky Lake fishery, economic yield is largely a function of roe yield since the market price for roe is about 200 times that of flesh. Therefore, the economic yield plots in Figure 3 do not vary greatly from the patterns in roe yield depicted in

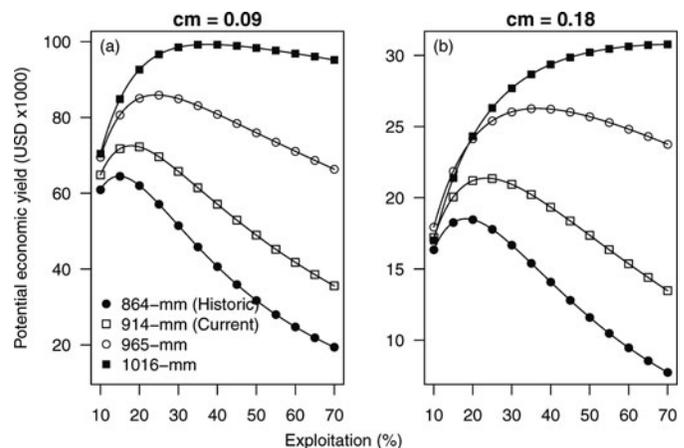


FIGURE 3. Potential economic yield of combined roe and flesh of Paddlefish harvested under four minimum eye-to-fork length limits (mm) at two levels of conditional natural mortality (cm) and over a range of exploitation rates in Kentucky Lake. Predictions are based on 1,000 recruits and assume that fishers receive wholesale prices of US\$1.10 per kilogram for flesh and \$220 per kilogram for roe.

Figure 2. However, this illustration can potentially be useful in the management of mixed-tissue fisheries, especially if the ratio of flesh price : roe price changes, which may be the case if farm-raised Paddlefish can provide a reliable source of caviar (Mims 2001). Mixed-tissue fisheries are not limited to caviar-producing Paddlefish or sturgeon species; roe markets also exist for several marine and freshwater fishes, such as herrings *Clupea* spp., mullets (e.g., Striped Mullet *Mugil cephalus*), Alaskan Wall-eye Pollock *Gadus chalcogrammus*, and several salmon species (e.g., *Oncorhynchus* spp.). Additionally, this type of analysis could also be extended to other commercially harvested species, such as Goosefish *Lophius americanus* or cods *Gadus* spp., that support a market for flesh and liver.

Although the highest minimum length limit (1,016 mm) produced the greatest roe yields and economic returns at most of the modeled u -values, there are at least three reasons why it will be difficult to achieve an increased length limit for Paddlefish in Kentucky Lake. First, after previously embracing a plan to gradually increase the minimum length limit from 864 mm (historic) to 965 mm, the commercial fishing industry in Tennessee subsequently lobbied to abandon that management action and to hold the limit at 914 mm EFL. It is unlikely that the industry will suddenly reverse course and embrace a higher minimum length limit. Secondly, raising the minimum length limit will likely increase the bycatch of sublegal Paddlefish, potentially leading to an increase in discard mortality. Lastly, Tennessee fishers have recently been allowed to check captured fish for roe by using a large-bore needle and syringe prior to harvest—a practice that is viewed as a conservation measure among fishers (Scholten 2009). Returning non-roe-producing Paddlefish back into the population was not accounted for in our model. However, this practice should increase roe yield and reduce the potential for growth overfishing and recruitment overfishing over the simulated range of minimum length limits and u -values, assuming there is no bycatch or discard mortality. Although most of the released Paddlefish will survive at cool water temperatures, discard mortality can exceed 70% with the warm temperatures that typically occur at the end of the fishing season (Bettoli and Scholten 2006). The prevalence among fishers of checking Paddlefish for roe and the effects of discard mortality on yield dynamics are uncertain and will require further research.

Greater flexibility and biological realism in underlying weight-at-age functions can be evaluated by using numerical integration to predict yield. Historically, evaluation of integrals was limited to analytical solutions or approximations. The best example of this was the original analytical solution for the equilibrium yield model presented by Beverton and Holt (1957). This solution could predict equilibrium yield, but it required the unrealistic assumption of isometric scaling of fish weight with length. Using an incomplete beta function, Jones (1957) provided an approximation to the equilibrium yield function that allowed allometric scaling of weight with length, thus conferring increased biological realism to equilibrium yield predictions. Numerical integration can be used to evaluate very complex

biomass and yield dynamics, representing increased biological realism for which analytical solutions or approximations likely do not exist. Specifically, this approach can potentially accommodate variable rates of natural mortality and fishing mortality or fishery recruitment (e.g., knife edge or continuous). The improved biological realism afforded by the use of numerical integration to solve the equilibrium roe yield model provided a better understanding of potential growth overfishing in this mixed-tissue fishery.

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