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ARTICLE

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Abstract

Fish age and length at 50% maturity are used extensively in the management of exploited fish populations. These parameters are historically estimated using logistic regression models (e.g., frequentist inference) for individual year-classes and often fail to converge or result in insignificant results when a small sample size is used. The sample-size problem motivated us to evaluate whether a hierarchical logistic regression model fit using frequentist inference or Bayesian inference, could improve our ability to fit these models. Our objective was to compare Bayesian and frequentist inference for estimating age and length at 50% maturity to determine whether the models produced similar values. To make this evaluation, we used a long-term data set of Yellow Perch *Perca flavescens* from southern Lake Michigan. Frequentist inference of the year-class-specific models resulted in significant results when sample size was sufficiently large, a result that occurred in 76% of the models. The hierarchical model produces estimates of age (or length) at 50% maturity for all year-classes using both frequentist and Bayesian inference. However, Bayesian inference of the hierarchical model resulted in more precise parameter estimates and provided the complete posterior distribution in one seamless and easy approach, and the computation time was 78% to 83% faster. We suggest that a hierarchical model fit using Bayesian inference of age (or length) at 50% maturity is an improvement over frequentist interference methods by providing more information about the population of interest, particularly when sample sizes are limited.

Fish age and length at maturity are used extensively in the management of fish populations (Shephard and Jackson 2005; Wilberg et al. 2005; Schill et al. 2010; Stark 2012). These values are traditionally identified by estimating age or length at 50% maturity (Shephard and Jackson 2005; Stark 2012), but for the purposes of modeling population dynamics this value is often assumed constant and based on historical data collections (Jennings et al. 1999; Wilberg et al. 2005). Age (or length) at 50% maturity describes the point at which 50% of the population is mature.

The logistic regression model is commonly used to make these estimations (Cook et al. 1999), and maturity is expressed as a binary value of either 1 (mature) or 0 (immature). Parameters of the logistic regression model are traditionally estimated using maximum likelihood techniques that are common in most statistical packages (e.g., SAS: PROC LOGISTIC, R–glm(), and STATA–logit). However, the maximum likelihood estimates require a relatively large sample size for convergence (Peduzzi et al. 1996; Greenland et al. 2000). When the events per predictor variable are fewer than 10, regression coefficients are biased and confidence limits around the estimated parameters cannot be calculated (Peduzzi et al. 1996). Further, bias in the odds ratios from logistic regression has been detected with sample sizes as large as 100 (Nemes et al. 2009). Simulation studies evaluating bias of a frequentist hierarchical logistic regression suggested a minimum group size of 50 and 50 groups are needed for valid parameter estimates (Moineddin et al. 2007). This event and group-size threshold can be problematic with fish data sets that include year-classes with poor recruitment (O'Brien 1999; Wang et al. 2009) or limited sampling, resulting in incomplete descriptions of maturity.

The sample size problem associated with maximum likelihood estimates (e.g., frequentist inference) of the logistic regression model motivated us to evaluate the use of Bayesian

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inference to derive estimates of age and length at 50% maturity. Bayesian inference is a fundamentally different way to describe probability (Ellison 1996). Under the Bayesian framework, parameters are considered random and data are considered fixed; whereas, the frequentist inference approach considers the parameters as fixed unknowns and the data random. Bayesian inference results in posterior distributions of a parameter and makes a direct probability statement of the parameter of interest, while frequentist inference results in point estimates with 95% confidence intervals that are based on hypothetical replicates and do not make a direct statement about the true parameter.

The use of Bayesian inference has dramatically increased over the past 20 years, particularly in ecological studies (Reckhow 1990; McCarthy 2007; Royle and Dorazio 2008, Kéry 2010, Kéry and Schaub 2012). In fisheries management, Bayesian inference has been applied to stock assessments (Chen et al. 2003; Wilberg et al. 2005), estimates of sport fish abundance from stream depletion sampling (Mäntyniemi et al. 2005; Ruiz and Laplanche 2010), estimates of annual growth variation using the von Bertalanffy growth function (He and Bence 2007), and determination of Brook Trout *Salvelinus fontinalis* population structure from genotypic data (Rogers and Curry 2004). Bayesian methods are also discussed as an alternative to maximum likelihood estimates in advanced fisheries text books (e.g., Quinn and Deriso 1999; Brown and Guy 2007).

The foundation of Bayesian inference is based on Bayes' theorem where the probability of a model parameter (θ) given the observed data (X) is estimated using the data, the prior belief about θ, and the evidence. Bayes' theorem states the posterior distribution of the model parameters is calculated by

$$p(\theta|X) = \frac{p(X|\theta)\, p(\theta)}{\int d\theta p(X|\theta)\, p(\theta)}, \tag{1}$$

where $p(\theta|X)$ denotes the posterior distribution of the parameter given the data, $p(\theta|X)$ denotes the probability of the data given the parameter (i.e., the likelihood function), $p(\theta)$ denotes the prior probability of the model parameter, and the denominator (the evidence) is a normalizing parameter calculated by summing across all possible parameter values weighted by the strength of their belief. For a thorough discussion on Bayesian inference see Gelman et al. (2004) and Kruschke (2011).

Bayesian inference predates frequentist inference methods (Bayes and Price 1763); however, until recently the computations required were too great for most computers. Beginning in the 1990s modern advances in computing speed, Markov chain Monte Carlo (MCMC) algorithms, and the BUGS language brought Bayesian methods within reach to many non-mathematicians (Gilks et al. 1996; Lunn et al. 2000). Bayesian inference can now be conducted using a variety of software that requires only pseudocode to represent the model (Lunn et al. 2000; Plummer 2003; Stan Development Team 2012).

The objective of this study was to evaluate estimation of age and length at 50% maturity from a long-term Yellow Perch *Perca flavescens* data set using frequentist inference of individual-level regressions, frequentist inference of a hierarchical model, and Bayesian inference of a hierarchical model. We hypothesize Bayesian inference will provide similar results to the frequentist inference model when a sufficient sample size is used. However, we also hypothesize when sample sizes are limited, Bayesian inference will provide usable results, in contrast to the frequentist inference models.

METHODS

Data.—The data set format consists of n_j individuals sampled from year-class j. For each individual i the maturity state Y_i was recorded as a binary outcome of mature (1) or immature (0). We used a long-term monitoring data set of Yellow Perch from southern Lake Michigan (Lauer and Doll 2012) to evaluate the two methods of statistical inference. Yellow Perch were sampled in early and late June in southern Lake Michigan at up to three sites between 1984 and 2009, resulting in six samples per year. Multifilament gill nets were set at 10- and 15-m depths and fished for approximately 12 h. In addition, a semiballoon bottom trawl was towed at the 5-m depth contour at night for 1 h each sample date. From 1984 to 1988 only two sites were sampled resulting in a total gill-net effort of four net-nights per year and 4 h of trawling per year. From 1989 to 2009, three sites were sampled resulting in a total gill-net effort of six net-nights per year and 6 h of trawling per year. See Lauer and Doll (2012) for a detailed description of the sampling protocol.

At the conclusion of each sample, fish ≥age 1 collected in the trawl and gill nets were measured for TL, weight, sex, and maturity following Treasurer and Holliday (1981). When more than 300 fish were captured, a subsample of 300 Yellow Perch was randomly selected for measurement. Individuals ≥age 1 were differentiated from age-0 fish by size.

Yellow Perch aging structures were removed from up to 10 individuals in each 10-mm length class each year. Scales from samples in 1984–1993 and opercular bones for samples from 1994 to 2009 were aged independently by two readers. Aging methods were changed in 1994 as opercular bones were shown to have a lower coefficient of variation when compared with scales (Baker and McComish 1998). Discrepancies were discussed by both readers until a consensus was reached. Only fish where the maturity status and age were known were used in this analysis. Males and females were analyzed separately due to known sexual dimorphism (Headley and Lauer 2008).

General maturity model description.—Maturity state is modeled using logistic regression where the probability of an individual being mature is assumed to follow the Bernoulli distribution,

$$Y_{ij} \approx \text{Bernoulli}\,(\pi_{ij}), \tag{2}$$

where π_{ij} is the probability of individual i of year-class j being mature. The Bernoulli parameter π_{ij} is then modeled as a linear function of covariate x_{ij} (e.g., age and length, modeled separately) with the logit link so that

$$\begin{aligned} Y_{ij}|x_{ij}\alpha_j, \beta_{1j} &\approx \text{Bernoulli [logistic}\,(\alpha_j + \beta_{1j}x_{ij})], \\ \alpha_j &\approx N(\theta, \sigma^2), \quad \text{and} \\ \beta_{1j} &\approx N\big(\theta_1, \sigma_1^2\big), \end{aligned} \tag{3}$$

where α_i is the intercept parameter of year-class j and assumed to follow a normal distribution with mean θ and variance σ^2, β_{1j} is the log odds parameter of the logistic regression model and represents the effect of the age or length, x_{ij} on the logit of π_{ij}, and is assumed to follow a normal distribution with mean θ_1 and variance σ_1^2. Estimates of age and length at 50% maturity for year-class j (i.e., inflection point of the curve) are derived using the equation $-\alpha_j/\beta_{1j}$. Estimates of age and length at 50% maturity were calculated for each year-class.

Frequentist inference.—Individual frequentist models were fit to each year-class and sex using the glm() function with the binomial distribution and logit link in R version 2.15.3. Bootstrap parameter estimates were used to derive 95% CIs for the maturity index using the boot package (Canty and Ripley 2012). For each cohort where n_j individuals were sampled, n_j individuals were selected at random with replacement. The resampled data set was used to derive age (or length) at 50% maturity as described above. The process was repeated to obtain 1,000 replicates and the resulting distribution of the estimated age (or length) at 50% maturity was used to derive the 95% CIs. An alpha level was set at 0.05 to determine statistical significance for frequentist results.

The hierarchical model was fit to all year-classes combined for each sex using the lmer() function with the binomial distribution and logit link in R version 2.15.3 (Appendix 1). Here, the intercept and slope are given a grouping variable, year-class, where both are allowed to vary. Thus, the frequentist hierarchical model is now a varying-intercept and varying-slope model with year-class as a random effects grouping variable (Gelman and Hill 2007). Bootstrap parameter estimates were used to derive 95% CIs for the year-class-specific maturity index using the boot package similar to the single level models (Appendix 2).

Bayesian inference.—Parameters were estimated using Bayesian inference through a hierarchical framework so that parameters for each year-class were randomly drawn from the same probability distribution. That is, the hyperpriors (θ, θ_1, σ^2, and σ_1^2) represent the global distributions from which the year-specific mean and variance of the regression coefficients (α and β_1) are drawn. The hierarchical model allows year-classes with a small sample size to borrow strengths from data-rich years. We used MCMC simulations to estimate posterior probability intervals of model parameters using the JAGS version 3.3.0 software (Plummer 2003) implemented in R version 2.15.3 (R Development Core Team 2013). Within R, JAGS was called using the rjags package (Plummer 2012). We ran three MCMC chains for a total of 100,000 steps, sampling every step and discarding the first 10,000 steps as a burn-in period. The burn-in period is necessary to reduce the effect of the starting values on the MCMC results (Gelman et al. 2004). Parameters were given a noninformative prior distribution (Table 1). To determine whether the prior distributions specified for the model parameters were influencing the results more than were the data we ran each model a second time assuming a t-distribution rather than a normal distribution. The Student t-distribution allows for more extreme data points. Similar results from both models would suggest the data contain enough information to overcome information in the prior distribution. Bayesian parameter estimates were generated using the JAGS language; complete model specifications can be found in Appendix 3. Convergence of the MCMC algorithm was checked using the Brooks–Gelman–Rubin (BGR) scale-reduction factor (Brooks and Gelman 1998). The BGR factor is the ratio of between-chain variability to within-chain variability. When the chains have mixed well, there is not more variability between chains than within chains. Convergence is obtained when the upper limit of the BGR factor is close to 1.00.

TABLE 1. Prior distributions used for the Bayesian hierarchical logistic regression model.

Parameter	Prior distribution
Year-class level	
α_j	Normal (θ, σ^2)
β_{1j}	Normal (θ_1, σ_1^2)
Global level: hyperpriors	
θ	Normal (0, 1000)
θ_1	Normal (0, 1000)
σ^2	Uniform (0,10)
σ_1^2	Uniform (0,10)

Inference comparisons.—Inherent differences exist in the definition of probability between Bayesian posterior distributions and frequentist point estimates with 95% CIs. Therefore, we focused on their respective interpretation used in making management decisions for comparisons. Additionally, mean point estimates from the results of the hierarchical model fit with frequentist inference are compared with the median estimates of the posterior distribution from hierarchical model fit with Bayesian inference using root mean squared error (RMSE). The RMSE is calculated using the equation

$$\text{RMSE} = \sqrt{\frac{1}{n}\sum_{i=1}^{n}(\text{FM}_i - \text{BM}_i)^2}, \tag{4}$$

where n = number of year-classes, FM_i = frequentist estimate of age (or length) at 50% maturity, and BM_i = Bayesian inference estimate of age (or length) at 50% maturity. The RMSE is on the same scale as the original units; therefore, the value represents the number by which the estimates of age (years) and length (mm) differ. Parameter estimation time for bootstrap CIs from the hierarchical model fit with frequentist inference and Bayesian inference will also be used as a benchmark for evaluation. The time required for the individual glm() and lmer() functions to complete is minimal; thus, they are not included in the total time to analyze the data using frequentist methods. The computer used for this analysis was a Dell Precision model M 6700 (64-bit, 32 GB RAM, and Intel Core i7 2.70 GHz processor, Windows 7 Professional operating system).

RESULTS

A total of 5,465 Yellow Perch (3,321 females and 2,144 males) were included in the analysis (Table 2), and generally more mature fish than immature fish were collected for each year-class. Females consisted of 61% mature individuals and males consisted of 80% mature individuals. Four year-classes of females and five year-classes of males had fewer than 10 individuals in either the mature or immature category.

TABLE 2. Total number of mature and immature females and male Yellow Perch, by year-class, sampled from southern Lake Michigan.

	Females		Males	
Year-class	Mature	Immature	Mature	Immature
1984	92	51	101	21
1985	76	53	52	26
1986	77	28	75	7
1987	56	22	64	11
1988	117	85	128	45
1989	69	52	95	21
1990	61	59	94	14
1991	20	61	61	14
1992	15	4	21	1
1993	33	41	34	27
1994	99	27	61	19
1995	194	79	120	15
1996	71	17	43	0
1997	193	82	120	28
1998	454	161	274	21
1999	82	27	36	11
2000	86	21	40	1
2001	107	73	56	12
2002	61	136	82	30
2003	25	93	72	30
2004	16	37	44	18
2005	3	39	34	13
2006	0	43	18	21
2007	5	18	0	13
Total	2,012	1,309	1,725	419

Frequentist Inference

Frequentist estimates of the individual maturity models resulted in significant parameter estimates for 73 of the 96 models (76%; Table 3). Estimates of female age and length at 50% maturity ranged from 2.2 to 4.7 years and from 154 to 202 mm (Table 3). Male age and length at 50% maturity ranged from 1.1 to 2.3 years and from 90 to 129 mm (Table 3).

The hierarchical model estimated parameters for all year-classes; however, 95% CIs for all year-classes were large compared with parameters from Bayesian inference (Tables 4, 5). Estimates of female age and length at 50% maturity ranged from 1.0 to 5.8 years and from 157 to 201 mm (Figures 1A, 2A). Male age and length at 50% maturity ranged from 1.2 to 2.1 years and from 94 to 120 mm (Figures 1C, 2C).

Bayesian Inference

The Bayesian inference models converged after 100,000 iterations. The upper 95% CIs of the BGR factors for all model parameters was less than 1.15. Parameter estimates were nearly identical between noninformative normally distributed priors and noninformative *t*-distributed priors, suggesting the data contain enough information to overcome the prior distributions.

At the year-class level, maturity models showed that the variability in the effect of age was higher in females than males while there was no difference in variance in the effect of length. The median value of the hyperprior variance (σ_1^2) for female age was 0.917 (95% CI = 0.564–1.558) while that for males was 0.422 (95% CI = 0.204–0.801). The median value of the hyperprior variance ($\sigma_1{}^2$) for female length was 0.005 (95% CI = 0.001–0.009) while that for males was 0.007 (95% CI = 0.002–0.012). These results suggest there is a more consistent increase in the odds of a male being mature as age increases than there is for a female, while the effect of length is more consistent among year-classes. Precision as measured by 95% credible intervals were generally smaller than 95% CIs for all models (Tables 4, 5).

Posterior median estimates of female age and TL at 50% maturity ranged from 2.2 to 6.1 years and from 157 to 201 mm, respectively (Figures 1B, 2B). Posterior median estimates of male age and length at 50% maturity ranged from 1.2 to 2.2 years and from 92 to 122 mm, respectively (Figures 1D, 2D). Overall, the posterior median estimate of female age and length at 50% maturity was 3.3 years (95% CI = 2.6–4.3) and 178 mm, respectively (95% CI = 172–184). Posterior median male age and TL at 50% maturity was 1.6 years (95% CI = 1.4–1.8) and 105 mm (95% CI = 99–110), respectively.

Inference Comparisons

Mean estimates of the hierarchical model fit using frequentist inference were nearly identical to the median estimates of age and length at 50% maturity from Bayesian inference for most year-classes. The point estimates of age at 50% maturity differed at most by 2 years for females (RMSE = 0.41) and by 0.3 years

TABLE 3. Age (years) and length (TL, mm) at 50% maturity estimates of Yellow Perch from individual year-class logistic regression models using frequentist inference; upper and lower limit (±) of the 95% CI is in parentheses. Asterisk (*) indicates individual logistic regression models resulted in insignificant coefficients.

	Females		Males	
Year-class	Age	Length	Age	Length
1984	3.11 (±0.33)	154.41 (±6.61)	1.36 (±0.70)	105.48 (±12.23)
1985	3.71 (±0.41)	158.85 (±7.23)	2.27 (±0.52)	123.61 (±12.35)
1986	3.47 (±0.33)	164.94 (±11.45)	*	102.18 (±29.36)
1987	3.15 (±0.42)	172.01 (±9.61)	1.82 (±0.54)	115.5 (±15.88)
1988	3.17 (±0.12)	167.43 (±5.23)	1.97 (±0.28)	117.8 (±8.80)
1989	3.01 (±0.32)	164.5 (±7.80)	1.76 (±0.31)	110.6 (±12.35)
1990	3.14 (±0.28)	177.48 (±7.71)	1.43 (±0.43)	99.55 (±10.02)
1991	*	185.59 (±7.22)	1.29 (±0.56)	104.54 (±17.72)
1992	*	*	*	*
1993	2.51 (±0.51)	194.07 (±10.71)	*	129.08 (±12.87)
1994	2.19 (±0.21)	190.25 (±10.63)	*	*
1995	2.32 (±0.20)	192.17 (±5.10)	1.12 (±0.18)	99.85 (±9.55)
1996	2.64 (±0.43)	196.49 (±14.54)	*	*
1997	2.38 (±0.16)	201.55 (±6.53)	*	114.08 (±7.14)
1998	3.02 (±0.18)	176.83 (±4.16)	1.05 (±0.37)	95.54 (±7.92)
1999	3.69 (±0.61)	165.09 (±13.00)	1.25 (±0.93)	*
2000	3.68 (±0.60)	174.4 (±14.67)	*	*
2001	3.65 (±0.38)	189.19 (±6.36)	1.42 (±0.50)	95.76 (±15.29)
2002	4.74 (±0.47)	189.72 (±7.67)	1.83 (±0.22)	103.41 (±7.57)
2003	4.74 (±0.45)	177.37 (±7.09)	1.92 (±0.23)	99.81 (±7.60)
2004	4.26 (±0.68)	168.04 (±7.36)	1.69 (±0.38)	90.16 (±7.05)
2005	*	*	1.38 (±3.30)	91.24 (±11.44)
2006	*	*	1.69 (±0.54)	94.75 (±(8.89)
2007	*	*	*	*

for males (RMSE = 0.10). The point estimates of TL at 50% maturity differed at most by 14 mm for females (RMSE = 8.14) and 4 mm for males (RMSE = 1.30). Additionally the range of 95% credible intervals and 95% CIs were similar for all models (Figures 1, 2).

The computation time to conduct the bootstrap CIs of age at 50% maturity for the hierarchical model fit with frequentist inference was 22.5 min for females and 18.1 min for males. Bootstrap parameter estimates for TL at 50% maturity took 50.6 min for females and 25.8 min for males. Bayesian inference of the hierarchical model describing age at maturity finished in 3.8 min for females and 3.3 min for males. Bayesian inference of the hierarchical model describing length at maturity finished in 8.5 min for females and 5.8 min for males. Overall the computation time of Bayesian inference was 78% to 83% less than bootstrap CIs.

DISCUSSION

This study compared the performance of two statistical inference paradigms in the analysis of age and length at maturity. First we showed that when using traditional methods of statistical inference, a hierarchical approach is preferred over single-level logistic regressions, particularly when sample size is small. Further, our results showed that when using a hierarchical model similar age and length at 50% maturity estimates are produced by both frequentist and Bayesian inference. However, Bayesian inference resulted in more precise estimates of uncertainty around the model parameters, required one step in the modeling process, and provided the complete posterior distribution in one seamless and easy approach. Frequentist inference required a second step to generate CIs for estimates of age (or length) at 50% maturity. Further, the large 95% CIs from frequentist inference of parameter estimates suggest bootstrap CIs of the derived parameters (age or length at 50% maturity) are misleading (i.e., the high precision is biased). Finally, Bayesian inference finished as much as 83% faster than bootstrap estimates of 95% CIs.

Bayesian inference of the maturity model explicitly provides more information about the model and data in the global parameters (e.g., θ and θ_1); this is not easily gained through frequentist inference. These parameters represent the distribution of the parameters given the data and describe the most credible estimates

TABLE 4. Parameter estimates from the hierarchical logistic model describing female and male Yellow Perch age at maturity using frequentist and Bayesian inference. Numbers in parentheses are lower and upper limits of the 95% CIs (frequentist) and 95% credible intervals (Bayesian).

	Female age at maturity model				Male age at maturity model			
	Frequentist		Bayesian		Frequentist		Bayesian	
Year-class	Slope	Intercept	Slope	Intercept	Slope	Intercept	Slope	Intercept
1984	1.85 (–0.040, 3.742)	–5.78 (–7.674, –3.886)	1.92 (1.395, 2.568)	–5.96 (–7.955, –4.328)	1.41 (–0.044, 2.870)	–2.15 (–3.607, –0.693)	2.00 (1.432, 2.471)	–3.41 (–4.313, –2.175)
1985	1.65 (–0.373, 3.678)	–6.10 (–8.131, –4.069)	1.77 (1.280, 2.358)	–6.55 (–8.862, –4.642)	1.38 (0.063, 2.707)	–2.92 (–4.247, –1.593)	1.76 (1.291, 2.293)	–3.81 (–4.939, –2.882)
1986	2.12 (–0.466, 4.709)	–7.29 (–9.878, –4.702)	2.17 (1.545, 2.974)	–7.48 (–10.315, –5.244)	1.83 (–0.248, 3.917)	–3.09 (–5.173, –1.007)	2.13 (1.603, 2.702)	–3.72 (–4.957, –2.638)
1987	1.74 (–0.729, 4.214)	–5.57 (–8.045, –3.095)	1.84 (1.198, 2.595)	–5.87 (–8.339, –3.630)	2.09 (0.127, 4.056)	–3.62 (–5.581, –1.659)	2.17 (1.665, 2.781)	–3.79 (–5.077, –2.821)
1988	3.34 (0.491, 6.185)	–10.40 (–13.323, –7.477)	3.05 (2.322, 4.092)	–9.65 (–12.966, –7.296)	1.62 (0.396, 2.842)	–3.12 (–4.340, –1.900)	1.89 (1.471, 2.343)	–3.71 (–4.682, –2.861)
1989	2.03 (–0.201, 4.262)	–6.14 (–8.375, –3.905)	2.08 (1.490, 2.844)	–6.27 (–8.551, –4.449)	2.72 (0.835, 4.607)	–4.57 (–6.461, –2.679)	2.35 (1.847, 3.014)	–3.90 (–5.161, –3.045)
1990	2.55 (–0.046, 5.151)	–8.01 (–10.605, –5.415)	2.47 (1.814, 3.333)	–7.78 (–10.395, –5.766)	2.86 (0.899, 4.814)	–4.18 (–6.133, –2.227)	2.55 (2.000, 3.250)	–3.60 (–4.700, –2.639)
1991	2.63 (–0.684, 5.954)	–9.09 (–12.408, –5.772)	2.53 (1.714, 3.737)	–8.93 (–12.782, –6.299)	1.79 (0.158, 3.424)	–2.53 (–4.165, –0.895)	2.31 (1.671, 2.959)	–3.36 (–4.254, –2.250)
1992	3.44 (–1.431, 8.315)	–9.06 (–13.937, –4.183)	2.71 (1.605, 4.225)	–6.88 (–10.667, –3.944)	2.93 (0.172, 5.687)	–4.39 (–7.150, –1.630)	2.51 (1.824, 3.522)	–3.58 (–4.878, –2.290)
1993	2.66 (–0.103, 5.423)	–6.93 (–9.694, –4.166)	2.59 (1.809, 3.642)	–6.57 (–9.006, –4.642)	4.11 (1.960, 6.259)	–6.48 (–8.631, –4.329)	2.60 (1.998, 3.562)	–4.10 (–5.654, –3.220)
1994	3.16 (0.457, 5.859)	–7.10 (–9.798, –4.402)	2.89 (2.078, 3.902)	–6.30 (–8.643, –4.331)	3.70 (1.643, 5.757)	–5.49 (–7.543, –3.437)	2.66 (2.065, 3.579)	–3.85 (–5.166, –2.997)
1995	5.07 (2.142, 8.007)	–11.90 (–14.907, –8.893)	4.06 (3.136, 5.327)	–9.55 (–12.474, –7.349)	2.99 (1.328, 4.642)	–3.66 (–5.317, –2.003)	2.85 (2.196, 3.679)	–3.34 (–4.283, –2.332)
1996	2.28 (–0.909, 5.472)	–6.21 (–9.396, –3.024)	2.25 (1.423, 3.236)	–5.96 (–8.637, –3.663)	3.16 (0.329, 5.988)	–4.45 (–7.278, –1.622)	2.71 (2.013, 3.761)	–3.39 (–4.538, –1.834)
1997	2.87 (0.990, 4.757)	–6.92 (–8.804, –5.036)	2.76 (2.167, 3.458)	–6.58 (–8.279, –5.110)	3.90 (2.211, 5.597)	–5.23 (–6.921, –3.539)	2.93 (2.302, 3.889)	–3.74 (–4.974, –2.892)
1998	1.46 (0.589, 2.332)	–4.44 (–5.310, –3.570)	1.49 (1.251, 1.756)	–4.52 (–5.430, –3.696)	2.12 (0.887, 3.347)	–2.48 (–3.709, –1.251)	2.52 (1.932, 3.152)	–3.06 (–3.922, –2.031)
1999	1.42 (–0.729, 3.56)	–5.25 (–7.395, –3.105)	1.59 (1.062, 2.237)	–5.91 (–8.282, –3.829)	1.28 (–0.34, 2.904)	–1.80 (–3.422, –0.178)	2.36 (1.542, 3.193)	–3.21 (–4.095 –2.025)
2000	1.32 (–0.702, 3.336)	–4.93 (–6.944, –2.916)	1.47 (1.009, 2.038)	–5.53 (–7.855, –3.511)	2.73 (–0.027, 5.495)	–4.25 (–7.008, –1.492)	2.40 (1.678, 3.406)	–3.66 (–5.101, –2.440)
2001	1.18 (–0.051, 2.421)	–4.36 (–5.594, –3.126)	1.25 (0.952, 1.593)	–4.60 (–5.938, –3.407)	2.12 (0.342, 3.896)	–3.15 (–4.925, –1.375)	2.35 (1.747, 3.058)	–3.50 (–4.482, –2.471)
2002	0.98 (–0.185, 2.136)	–4.62 (–5.779, –3.461)	1.05 (0.790, 1.337)	–4.94 (–6.225, –3.816)	2.34 (0.744, 3.943)	–4.14 (–5.737, –2.543)	2.22 (1.776, 2.809)	–3.91 (–5.103, –3.070)
2003	1.35 (–0.449, 3.141)	–6.33 (–8.124, –4.536)	1.52 (1.103, 2.019)	–7.17 (–9.379, –5.344)	2.62 (0.86, 4.382)	–4.78 (–6.540, –3.020)	2.26 (1.794, 2.905)	–4.078 (–5.468, –3.193)
2004	1.61 (–0.899, 4.121)	–6.61 (–9.121, –4.099)	1.86 (1.257, 2.641)	–7.76 (–11.336, –5.202)	2.71 (0.741, 4.676)	–4.42 (–6.391, –2.449)	2.36 (1.834, 3.053)	–3.810 (–5.052, –2.930)
2005	1.23 (–1.823, 4.274)	–5.89 (–8.936, –2.844)	1.65 (0.819, 2.696)	–7.78 (–11.847, –4.813)	1.73 (–0.025, 3.491)	–2.62 (–4.373, –0.867)	2.20 (1.608, 2.783)	–3.479 (–4.449, –2.364)
2006	0.98 (–2.979, 4.932)	–5.65 (–9.608, –1.692)	1.22 (–0.549, 2.617)	–8.29 (–12.970, –4.948)	1.78 (0.185, 3.366)	–2.91 (–4.505, –1.315)	2.16 (1.548, 2.792)	–3.553 (–4.489, –2.586)
2007	–2.17 (–5.082, 0.736)	2.09 (–0.823, 5.003)	0.34 (–1.883, 1.863)	–2.27 (–5.243, 1.547)	3.09 (0.571, 5.618)	–5.21 (–7.735, –2.685)	2.07 (1.058, 2.936)	–4.075 (–5.803, –3.133)

TABLE 5. Parameter estimates from the hierarchical logistic model describing female and male Yellow Perch length at maturity using frequentist and Bayesian inference. Numbers in parentheses are lower and upper limits of the 95% CIs (frequentist) and 95% credible intervals (Bayesian).

	Female length at maturity model				Male length at maturity model			
	Frequentist		Bayesian		Frequentist		Bayesian	
Year-class	Slope	Intercept	Slope	Intercept	Slope	Intercept	Slope	Intercept
1984	0.106 (–1.054, 1.266)	–16.68 (–17.837, –15.523)	0.103 (0.091, 0.118)	–16.24 (–18.430, –14.230)	0.074 (–2.035, 2.182)	–7.91 (–10.016, –5.804)	0.081 (0.070, 0.092)	–8.69 (–9.925, –7.534)
1985	0.104 (–1.066, 1.275)	–16.80 (–17.971, –15.629)	0.102 (0.090, 0.116)	–16.46 (–18.540, –14.500)	0.066 (–1.999, 2.131)	–7.88 (–9.942, –5.818)	0.074 (0.064, 0.086)	–8.93 (–10.490, –7.746)
1986	0.101 (–1.090, 1.292)	–16.92 (–18.107, –15.733)	0.100 (0.089, 0.113)	–16.7 (–18.740, –14.780)	0.072 (–2.237, 2.380)	–7.86 (–10.168, –5.552)	0.079 (0.068, 0.091)	–8.76 (–10.090, –7.561)
1987	0.098 (–1.093, 1.290)	–16.99 (–18.179, –15.801)	0.098 (0.088, 0.109)	–16.92 (–18.890, –15.110)	0.074 (–2.196, 2.344)	–8.29 (–10.556, –6.024)	0.078 (0.067, 0.090)	–8.85 (–10.290, –7.669)
1988	0.101 (–1.067, 1.270)	–17.05 (–18.218, –15.882)	0.100 (0.089, 0.112)	–16.84 (–18.840, –15.060)	0.059 (–1.665, 1.783)	–6.99 (–8.717, –5.263)	0.073 (0.063, 0.084)	–8.77 (–10.090, –7.599)
1989	0.101 (–1.080, 1.281)	–16.79 (–17.973, –15.607)	0.100 (0.089, 0.112)	–16.60 (–18.610, –14.700)	0.084 (–2.141, 2.309)	–9.03 (–11.254, –6.806)	0.082 (0.071, 0.094)	–8.80 (–10.150, –7.634)
1990	0.097 (–1.090, 1.284)	–17.17 (–18.358, –15.982)	0.097 (0.087, 0.109)	–17.16 (–19.170, –15.380)	0.090 (–2.253, 2.433)	–9.12 (–11.466, –6.774)	0.086 (0.074, 0.10)	–8.63 (–9.912, –7.374)
1991	0.093 (–1.104, 1.290)	–17.32 (–18.513, –16.127)	0.094 (0.083, 0.106)	–17.57 (–19.760, –15.710)	0.069 (–2.18, 2.317)	–7.45 (–9.701, –5.199)	0.080 (0.069, 0.093)	–8.66 (–9.897, –7.471)
1992	0.098 (–1.136, 1.331)	–17.07 (–18.304, –15.836)	0.098 (0.086, 0.112)	–17.04 (–19.250, –14.990)	0.091 (–2.661, 2.843)	–9.24 (–11.995, –6.485)	0.086 (0.071, 0.104)	–8.63 (–9.955, –7.244)
1993	0.091 (–1.122, 1.304)	–17.33 (–18.546, –16.114)	0.093 (0.082, 0.105)	–17.66 (–20.070, –15.710)	0.074 (–2.163, 2.312)	–8.88 (–11.114, –6.646)	0.075 (0.063, 0.088)	–9.05 (–10.760, –7.837)
1994	0.091 (–1.112, 1.294)	–17.21 (–18.409, –16.011)	0.093 (0.082, 0.104)	–17.52 (–19.760, –15.610)	0.092 (–2.484, 2.667)	–9.74 (–12.316, –7.164)	0.081 (0.069, 0.096)	–8.87 (–10.320, –7.692)
1995	0.092 (–1.099, 1.283)	–17.46 (–18.653, –16.267)	0.093 (0.083, 0.105)	–17.74 (–20.040, –15.820)	0.091 (–2.41, 2.593)	–9.24 (–11.741, –6.739)	0.086 (0.073, 0.100)	–8.65 (–9.908, –7.446)
1996	0.089 (–1.122, 1.301)	–17.28 (–18.495, –16.065)	0.092 (0.081, 0.104)	–17.71 (–20.150, –15.740)	0.089 (–2.616, 2.794)	–9.14 (–11.847, –6.433)	0.085 (0.071, 0.104)	–8.67 (–10.050, –7.258)
1997	0.086 (–1.111, 1.284)	–17.34 (–18.535, –16.145)	0.089 (0.079, 0.102)	–17.94 (–20.550, –15.860)	0.09 (–2.181, 2.361)	–9.89 (–12.157, –7.623)	0.081 (0.070, 0.094)	–8.93 (–10.390, –7.766)
1998	0.096 (–1.048, 1.239)	–16.97 (–18.113, –15.827)	0.096 (0.087, 0.107)	–17.03 (–18.880, –15.350)	0.092 (–2.085, 2.269)	–9.00 (–11.181, –6.819)	0.088 (0.076, 0.101)	–8.54 (–9.794, –7.279)
1999	0.101 (–1.083, 1.285)	–16.73 (–17.910, –15.550)	0.099 (0.088, 0.113)	–16.55 (–18.560, –14.620)	0.101 (–2.611, 2.813)	–9.78 (–12.492, –7.068)	0.089 (0.075, 0.105)	–8.58 (–9.846, –7.290)
2000	0.097 (–1.106, 1.301)	–17.04 (–18.246, –15.834)	0.097 (0.087, 0.109)	–17.03 (–19.050, –15.160)	0.090 (–2.590, 2.769)	–9.20 (–11.879, –6.521)	0.085 (0.071, 0.103)	–8.67 (–10.060, –7.297)
2001	0.092 (–1.099, 1.282)	–17.26 (–18.448, –16.072)	0.093 (0.083, 0.104)	–17.58 (–19.730, –15.690)	0.082 (–2.270, 2.434)	–8.27 (–10.617, –5.923)	0.085 (0.073, 0.100)	–8.56 (–9.805, –7.265)
2002	0.090 (–1.091, 1.272)	–17.03 (–18.215, –15.845)	0.092 (0.082, 0.103)	–17.4 (–19.420, –15.560)	0.091 (–2.141, 2.323)	–9.37 (–11.605, –7.135)	0.085 (0.074, 0.097)	–8.71 (–9.963, –7.546)
2003	0.097 (–1.087, 1.280)	–17.21 (–18.399, –16.021)	0.097 (0.087, 0.108)	–17.23 (–19.270, –15.490)	0.098 (–2.204, 2.399)	–9.74 (–12.044, –7.436)	0.087 (0.076, 0.101)	–8.67 (–9.928, –7.468)
2004	0.101 (–1.094, 1.295)	–16.98 (–18.179, –15.781)	0.099 (0.089, 0.113)	–16.8 (–18.810, –14.920)	0.103 (–2.324, 2.530)	–9.70 (–12.131, –7.269)	0.092 (0.078, 0.107)	–8.49 (–9.753, –7.119)
2005	0.097 (–1.101, 1.295)	–17.06 (–18.260, –15.860)	0.097 (0.085, 0.109)	–17.1 (–19.110, –15.280)	0.094 (–2.390, 2.579)	–9.05 (–11.535, –6.565)	0.090 (0.076, 0.104)	–8.49 (–9.750, –7.128)
2006	0.093 (–1.133, 1.319)	–17.23 (–18.459, –16.001)	0.094 (0.08, 0.107)	–17.5 (–20.180, –15.550)	0.093 (–2.418, 2.603)	–9.05 (–11.562, –6.538)	0.088 (0.075, 0.103)	–8.55 (–9.799, –7.314)
2007	0.099 (–1.117, 1.315)	–16.99 (–18.209, –15.771)	0.098 (0.086, 0.113)	–16.93 (–19.010, –14.960)	0.087 (–2.678, 2.852)	–9.26 (–12.020, –6.500)	0.080 (0.063, 0.097)	–8.85 (–10.390, –7.647)

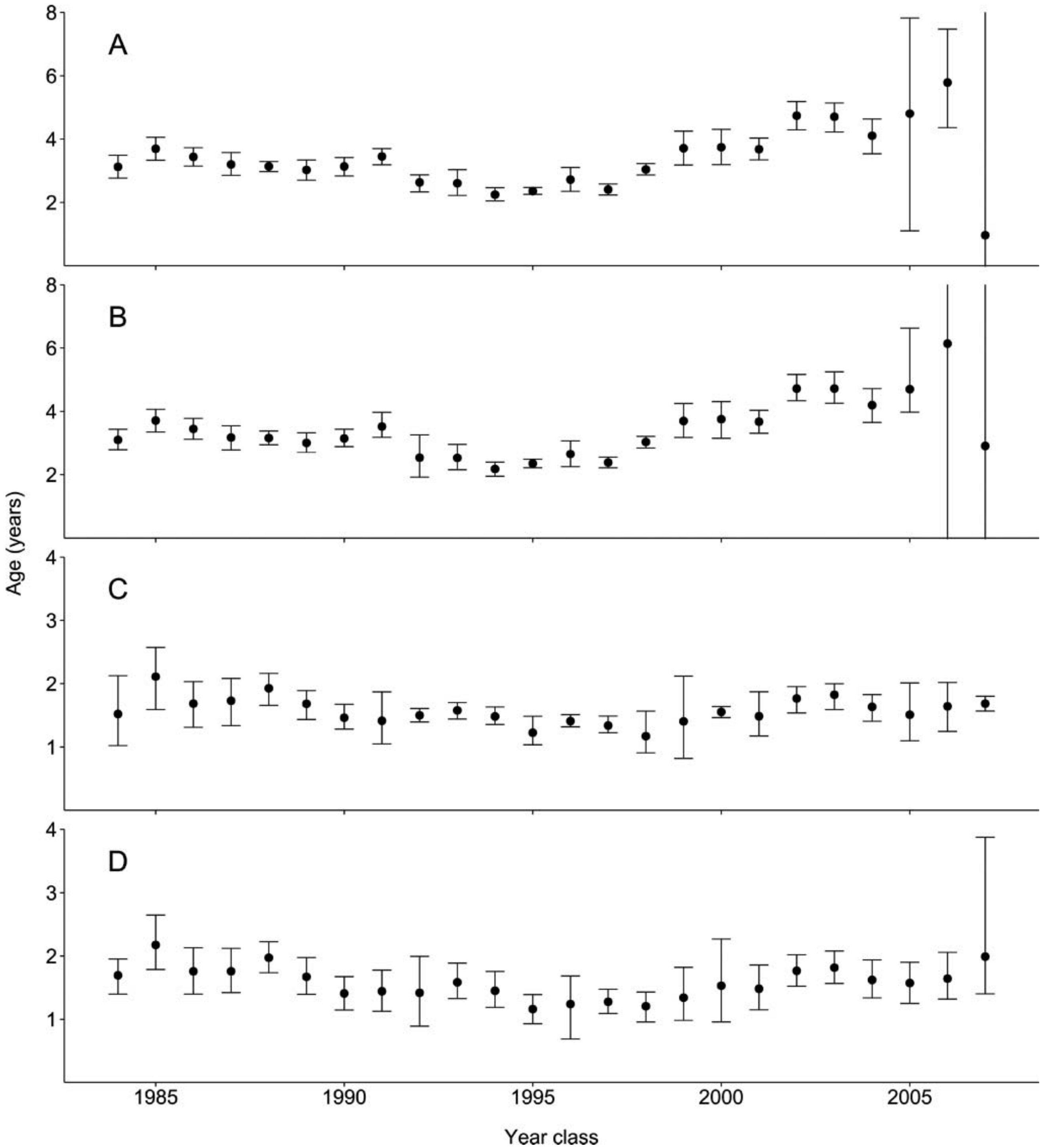

FIGURE 1. Female and male Yellow Perch age at 50% maturity estimates from hierarchical model by year-class. Frequentist inference results of (**A**) females and (**C**) males display the mean estimated age at 50% maturity (black dots) and 95% bootstrap CIs (upper and lower vertical lines). Bayesian inference results for (**B**) females and (**D**) males display the median estimated age at 50% maturity (black dots) and 95% credible intervals (upper and lower vertical lines).

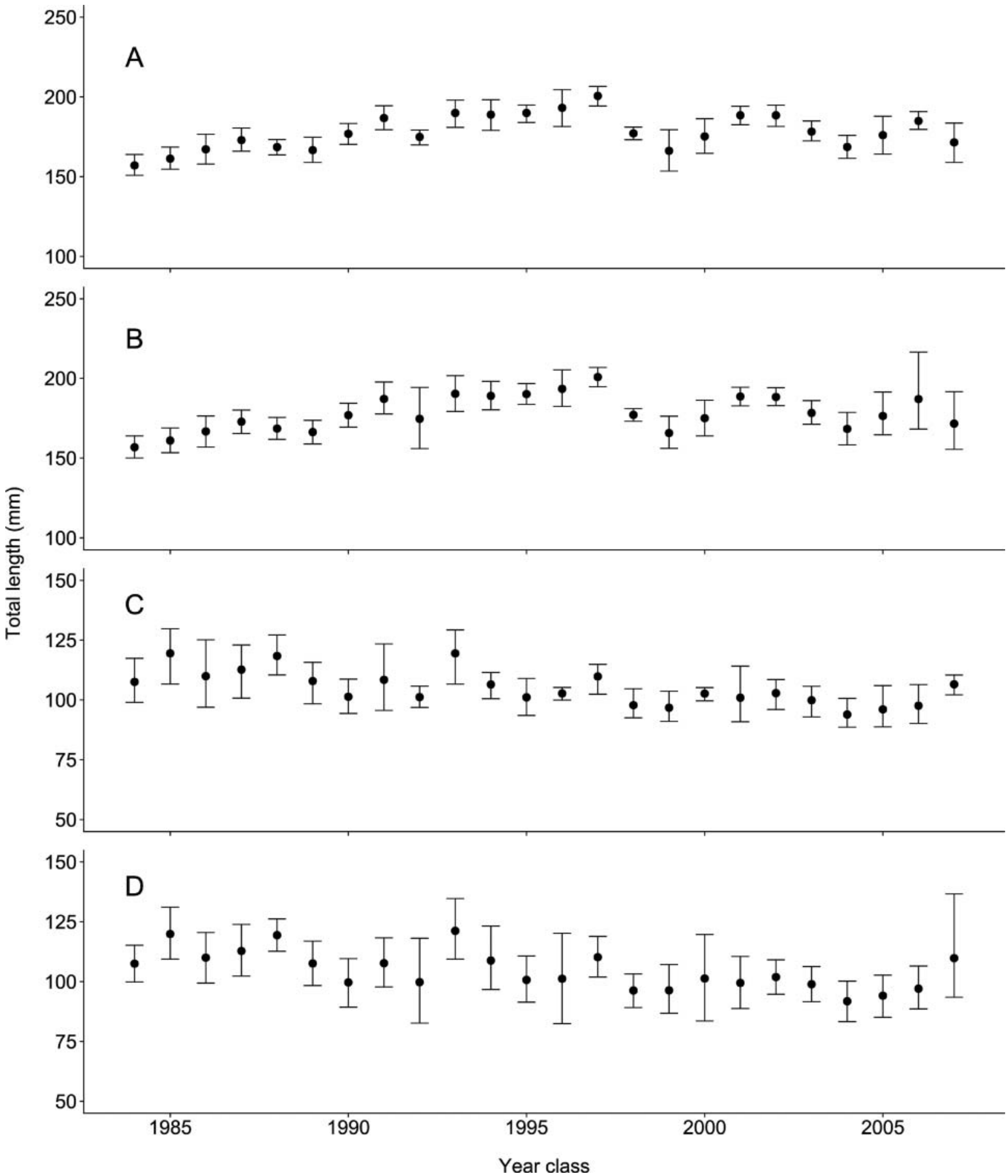

FIGURE 2. Female and male Yellow Perch length at 50% maturity estimates from hierarchical model by year-class. Frequentist analysis results of (**A**) females and (**C**) males display the mean estimated length at 50% maturity (black dots) and 95% bootstrap CIs (upper and lower vertical lines). Bayesian inference results of (**B**) females and (**D**) males display the median estimated length at 50% maturity (black dots) and 95% credible intervals (upper and lower vertical lines).

of age and length at 50% maturity. Analogous frequentist estimates require treating the estimated age and length at 50% maturity as fixed estimates with no variation and taking the average of bootstrap techniques, thus providing a biased estimate of uncertainty for the global maturity estimates. Additionally, bootstrap techniques require large data sets and few outliers, and assume no dependence structures (e.g., time series). In contrast, the Bayesian inference method provides a more direct measure of uncertainty. Further, if one chooses to conduct multiple post hoc comparisons among year-classes, *P*-values would have to be estimated for the frequentist approach and adjusted based on the number of comparisons the researcher intends to make. Bayesian inference does not suffer from this limitation and the posterior distribution of the parameters can be compared without penalizing for multiple comparisons (Kruschke 2010).

Variability of the parameters in the year-class level from Bayesian inference provided additional information that would be useful to managers while this information was lacking using frequentist inference. For example, knowing the variance in the log odds parameter of the age effect suggests the effect of age on female maturity is much more variable. Further, there were no differences in the variance of the effect of length suggesting factors that are influencing age rather than length at maturity have a greater impact on females than on males. Both parameters would be of great interest to managers to fully understand the life history of exploited fish. These parameters are not known using frequentist inference since the focus is on the point estimate of the log of the odds parameter rather than the distribution of credible values.

The model fit with Bayesian inference can easily be extended to assess a variety of hypotheses under one modeling framework. For example, adding group-level effects to the log odds parameter (β_{1j}) can test hypotheses regarding factors that best explain changes in the maturation rate. Two competing hypotheses have been proposed that can account for these changes (Law and Grey 1989; Law 2000; Heino et al. 2002). The first is a compensatory response hypothesis that predicts a phenotypic plastic response to a reduction in stock size. The reduced abundance results in higher growth rates, thus individuals more quickly attain the size required for maturation. This hypothesis could be tested for by including a group-level factor (i.e., year-class level) describing year-class strength. The second is an evolutionary response hypothesis that predicts individuals that have a late maturing phenotype are harvested, thus reducing the expected number of spawning for those individuals, resulting in generations that have the phenotype favoring maturation at earlier ages or smaller size. This hypothesis could be tested by including a group-level factor describing periods of increased harvest. Other possible extensions include modeling variability among year-classes as a function of covariates to test hypotheses regarding what factors are influencing the variation in the maturation rate among year-classes. Evaluating factors that influence how quickly fish mature or how variable the maturation rate is would be of great interest to fisheries managers.

Comparing frequentist and Bayesian inference is not new (Ghosh et al. 2006; Ismaila et al. 2007). Results of logistic regression using competing statistical paradigms have been evaluated in the pharmacology and clinical trial literature (Austin et al. 2001; Ambrose et al. 2012). However, to our knowledge this is the first study that compares results from a hierarchical logistic regression model fit using traditional frequentist and Bayesian inference in the fisheries literature.

Our results suggest that both inference methods are similar when fitting a hierarchical model; however, Bayesian inference provided more information about the data, was conducted in one seamless framework, and was completed in significantly less computational time. While concordant results were obtained, others have found discrepancies (Nielsen and Lewy 2002; Broomhall et al. 2010; Kruschke 2013). We suggest that Bayesian estimation of maturity indices using a hierarchical model is an improvement over frequentist methods by providing more information about the complete distribution of parameters and is not subject to secondary analysis to establish confidence intervals and *P*-values.

Two limiting factors to the widespread adoption of Bayesian inference have been computational time and familiarity with writing the necessary code. Both of these limitations are quickly eroding due to the continuous improvements in computer speed and emergence of programs that are easy to use. Computer memory is inexpensive and a standard personal computer with 4 GB of RAM and Microsoft Windows operating system can easily and quickly conduct Bayesian inference. While Bayesian inference using MCMC algorithms is usually considered slow, our results showed that the use of bootstrap techniques to generate CIs for frequentist inference can take significantly more time. Statistical packages such as R and SAS require the user to write code for their analysis. Any user familiar with these two languages should have no difficulty picking up the BUGS language and the code can often be less complex, as in our case where bootstrapping was necessary (Appendices 1–3). Finally, there has been recent focus to include programming skills into the curriculum of environmental science programs (Valle and Berdanier 2012). As more environmental scientists become comfortable with programming, taking advantage of Bayesian approaches will become much more within reach.

While this study focused on one population statistic, we suggest the statistical properties of other life history parameters that are routinely estimated for fisheries management purposes be evaluated using the Bayesian framework. For example, mortality estimates from catch curves, growth rates estimated from von Bertalanffy models, stock recruitment models, and population abundance estimates from depletion experiments are all commonly used in fisheries management. Most of the above-listed parameters have published methods using Bayesian inference (Mäntyniemi and Romakkaniemi 2002; Mäntyniemi et al. 2005; He and Bence 2007; Su and Peterman 2012). However, few go beyond describing their methods and detail how Bayesian and frequentist inference results differ.

Although there are fundamental differences between frequentist and Bayesian methods, it is important that natural resource managers identify advantages and disadvantages of each. Frequentist CIs and Bayesian credible intervals describe two different measures of uncertainty about a parameter of interest. However, both describe precision and could similarly be used to direct management recommendations. While the advantages of Bayesian inference are widely known (Beaumont and Rannala 2004; Kruschke 2013; this study) a thorough review of how it compares with frequentist inference may further enable the use of Bayesian methods, bringing this paradigm to the main stream of statistical inference in fisheries science. Ultimately, these comparisons may assist managers and researchers to better understand the complexity of data describing our natural resources.

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Appendix 1: Frequentist Inference Code for Model 3

Frequentist inference code for the hierarchical logistic regression model of length at maturity (model 3). Models of age at maturity are identical except age is substituted for length.

```
#load required packages
require(lme4)
require(arm)
#model statement with random effects for year-class.
mod1<-lmer(formula=mature~length + (1 + length|yc),data=
   data.name,family = binomial("logit"))
#extract slopes with 95%CI
df1<-data.frame() #data frame to hold slopes and 95%
   confidence intervals
for (i in 1:nrow(coef(mod1)$yc)){#loop to go through all year
   classes
est<-coef(mod1)$yc[i,2] #extract slope
ci<-coef(mod1)$yc[i,2] + c(-2,2)*se.ranef(mod1)$yc[i] #cal-
   culate 95% CI
ycci<-data.frame(slope=est,lci=ci[1],uci=ci[2]) #combine
infor-
   mation
df1<-rbind(df1,ycci) #send to data frame
}
#extract y-intercept with 95%CI
df2<-data.frame() #data frame to hold intercepts and 95%
   confidence intervals
for (i in 1:nrow(coef(mod1)$yc)){#loop to go through all year
   classes
est<-coef(mod1)$yc[i,1] #extract slope
ci<-coef(mod1)$yc[i,1] + c(-2,2)*se.ranef(mod1)$yc[i] #cal-
   culate 95% CI
yint<-data.frame(int=est,lci=ci[1],uci=ci[1]) #combine infor-
   mation
df2<-rbind(df2,yint) #send to data frame.
}
```

Appendix 2: Bootstrap Procedure for Estimating Confidence Interval

Bootstrap procedure for estimating 95% CIs for length at 50% maturity; model for age at maturity is identical except age is substituted for length.

```
#load required packages
require(lme4)
require(arm)
```

```
matfuncL<-function(dat,indices){#Function to pass through
    boot()
d<-dat[indices,]
modf<-lmer(formula=mature~length + (1 + lengthlyc),data
    =d,family=binomial("logit"))
coef<-coef(modf) #get coeficients
alpha<-as.numeric(coef$yc[,1]) #intercept
beta<-as.numeric(coef$yc[,2]) #log-odds
lmat<-(-alpha/beta) #calculated length at 50% maturity
rbind(lmat) #return 50% maturity
}
#bootstrap function
bootfuncL<-function(mod,dat){
#run bootstrap function on mixed model
mat.boot<-boot(dat=dat,statistic=matfuncL,R=50)
#initialize data frame to hold confidence intervals
ciop<-data.frame()
params<-c()
cis—<-data.frame()
#loop through bootstrap confidence intervals and combine data
for (i in 1:(ncol(mat.boot$t0))){#for i = 1 to number of year
    classes
matci<-boot.ci(mat.boot,type=c("norm"),index=i) #calculate
    95% confidence intervals
lci<-matci$normal[2] #extract lower confidence intervals
uci<-matci$normal[3] #extract upper confidence intervals
cis—<-data.frame(i=i,lci=lci,uci=uci) #organize 95% confi-
dence intervals
ciop<-rbind(ciop,cis—) #Combine 95% confidence intervals
}
mcoef<-coef(mod) #grab coeficients for each year-class
alpha<-as.numeric(mcoef$yc[,1]) #intercept
beta<-as.numeric(mcoef$yc[,2]) #slope
lmat<–alpha/beta #calculate length at maturity
for (i in 1:ncol(mat.boot$t0)){#loop through year classes and
    organize 50%maturity into a data frame
params<-rbind(params,lmat[i])
}
ciop<-cbind(ciop,params) #combine everything
return(ciop)
}
# length model
mod1<-lmer(formula=mature~length + (1 + lengthlyc),data
    =data.male,family=binomial("logit"))
#start timer and run bootrap analysis
Sys.time()->start
bootfuncL(mod=mod1,dat=data.name)
print(Sys.time()-start)
```

Appendix 3: JAGS Model Code

JAGS model code for the hierarchical logistic regression model.

```
model {
#hyperpriors
beta~dnorm(0,0.0001) #mean=0, precision=1/1000
sigma~dunif(0,10)
tau<-pow(sigma,-2)
beta1~dnorm(0,0.0001) #mean=0, precision=1/1000
sigma1~dunif(0,10)
tau1<-pow(sigma1,-2)
#Priors
for (j in 1:Y){
   b0[j]~dnorm(beta,tau)       #prior for year-class specific
                                  intercept parameter
   b1[j]~dnorm(beta1,tau1)     # prior for year-class specific log-
                                  odds parameter
}
#likelihood
for (i in 1:N){
    mat[i]~dbern(mu[i])            #maturity follows a Bernoulli
                                      distribution
    logit(mu[i])<-b0[yc[i]]        #logit link with linear
        + b1[yc[i]]*X[i]              function
}
#Derived parameter
for(k in 1:Y){
Ffiftymat[k]<-(-b0[k])/(b1[k])  #calculate age or length at
50% maturity from logistic regression parameters
}
avgFfiftymat <-(-beta + 0.0000001)/(beta1 + 0.0000001)
#overall age or length at 50% maturity for entire data set–a small
constant is added to the numerator and denominator to prevent
division by 0.
}
```