

FEATURE

Introduction to Bayesian Modeling and Inference for Fisheries Scientists

Jason C. Doll | Quantitative Fisheries Center, Department of Fisheries and Wildlife, Michigan State University, 375 Wilson Road, Room 100, East Lansing, MI 48824. E-mail: dolljas1@msu.edu

Stephen J. Jacquemin | Department of Biological Sciences, Wright State University–Lake Campus, Celina, OH

Photo credit: DaveAlan/Getty Images and Aleksandar Velasevic/iStockphoto (background image)

Bayesian inference is everywhere, from one of the most recent journal articles in *Transactions of the American Fisheries Society* to the decision-making process you undergo when selecting a new fishing spot. Bayesian inference is the only statistical paradigm that synthesizes prior knowledge with newly collected data to facilitate a more informed decision—and it is being used at an increasing rate in almost every area of our profession. Thus, the goal of this article is to provide fisheries managers, educators, and students with a conceptual introduction to Bayesian inference. We do not assume that the reader is familiar with Bayesian inference; however, we do assume that the reader has completed an introductory biostatistics course. To this end, we review the conceptual foundation of Bayesian inference without the use of complex equations; present one example of using Bayesian inference to compare relative weight between two time periods; present one example of using prior information about von Bertalanffy growth parameters to improve parameter estimation; and, finally, suggest literature that can help to develop the skills needed to use Bayesian inference in your own management or research program.

Bayesian inference is rooted in the notion that past experiences or information can be combined with new information to help explain certain events or inform the probability of outcomes associated with specific events. Although you might not be actively using Bayesian inference in your research, you are most likely using it in your everyday life. Bayesian inference is in the minds of card counters at the blackjack table, in the algorithm that selects the pop-up advertisements on your favorite social networking site, and in the unconscious decision-making process you undergo when you select a new fishing spot. It is a way of thinking and learning and has been proposed as the way our minds process information to make decisions (De Ridder et al. 2014). This natural way of thinking is in contrast to how many researchers analyze their data. For example, data are typically analyzed by calculating the probability of observing the data. This method of analyzing data is referred to as frequentist inference with null hypothesis statistical testing (NHST). When Bayesian inference is applied to data analysis, probabilities are assigned to certain outcomes given new information, and a decision is made based on the assigned probabilities.

If we used NHST in our everyday lives, we might find ourselves in a very disappointing situation. For example, suppose you are an avid Walleye *Sander vitreus* angler that is interested in fishing for nothing else. One day, while vacationing in Florida, you feel the itch to go fishing. However, after a lifetime of experience honing your Walleye fishing technique in the waters of your home state, Minnesota, you realize that you don't know how good the Walleye fishing is in Florida. Because you were trained as a frequentist and to use NHST, you decide to perform an experiment to determine the quality of Walleye fishing in Florida. Thus, you form a null hypothesis that fishing for Walleyes in Florida is no different than fishing for Walleyes in Minnesota. You know that you catch approximately one fish per hour of fishing effort, and based on your null hypothesis of no difference, you predict that you will catch one fish per hour of fishing in Florida. To test this hypothesis, you fish—for days—and catch no Walleyes. Minutes turn into hours, hours to days, and you catch no Walleyes; thus, your trip was a failure. After you have collected enough data from an array of Florida lakes, rivers, and swamps, you calculate that the probability of catching one Walleye per hour in Florida (your data) is so small if Walleye fishing in Florida is no different from Minnesota, that you conclude that Walleye fishing in Florida is NOT the same as Walleye fishing in Minnesota! Thus, the hypothesis that Walleye fishing in Florida is no different from Walleye fishing in Minnesota is rendered false (i.e., the null hypothesis is rejected). In this scenario, the time spent collecting new data to make a conclusion about Walleye fishing in Florida could have been reduced if our angler from Minnesota would have used prior

information on Walleye fishing in Florida. The reality is, however, that most of us looking to find a new fishing spot would just intuitively know to gather information before setting off to a new area for fishing. This information could come from reading blogs, overhearing conversations at the local fishing tackle shop (i.e., expert opinion), or examining distribution maps (i.e., published data). The point is that given a travel agenda in which the ability to search for a new Walleye fishing spot is limited, one would gravitate toward almost anywhere other than Florida—maybe the incredible spring Walleye fishery in western Lake Erie (Sandusky, Ohio) or even the St. Clair River run (southeastern Michigan).

Bayesian inference has been used to find lost ships, crack the “unbreakable” Enigma code of World War II, predict the outcomes of elections, forecast nuclear meltdowns, and predict Major League Baseball player performance (McGrayne 2012); it has also likely been used at some point in your own life to find a new fishing spot. Within our own field and more recently, Bayesian inference has been used in a variety of analyses, including generalized linear models, species distribution modeling, incorporating phylogeny into standard models describing trends in abundance, and stock assessments (Punt and Hilborn 1997; Jacquemin and Doll 2014; Rahikainen et al. 2014). Bayesian inference is all around us and is commonly used in fisheries science, yet many may not be familiar enough with it to appreciate (1) its flexibility for addressing both simple and complex problems and (2) how it can take advantage of all available information to help produce clear and direct inferences. Therefore, the obvious questions and focal points of this article become “What is Bayesian inference?”; “Why should I care about Bayesian inference?”; and “What can Bayesian inference do for me?” We attempt to answer these questions here.

The goal of this article is to provide fisheries managers, educators, and students with an introduction to Bayesian inference with minimal equations so that each reader can take the next step toward incorporating Bayesian inference into his or her quantitative toolbox, can be better prepared to critique research that uses Bayesian inference, and can teach the next generation of fisheries scientists. Herein, we provide a brief overview of what Bayesian inference is and demonstrate how Bayesian inference can be applied to fisheries data using two examples.

BAYESIAN INFERENCE What Is Bayesian Inference?

Bayesian inference uses a basic law of probability known as Bayes' theorem. Bayes' theorem was proposed by the Presbyterian minister Thomas Bayes more than 250 years ago and was later rediscovered in 1774 by Pierre Simon Laplace, who described it in scientific applications. This simple probability rule combines what we already know about an event with new information to provide an updated belief about that event.

Conceptually, what makes Bayesian methods unique is the incorporation of that prior information and reallocation of belief.

To better understand Bayesian inference, it is helpful to draw contrasts to what we already know (frequentist inference and NHST) from introductory biostatistics. Bayesian inference defines probability as a measure of belief about an event or model parameter (e.g., “What is the probability of mean catch rates increasing under the new management program?”). Bayesian inference uses Bayes’ theorem (see below) to combine new data and any prior information. New data and prior information are incorporated by describing each with a probability distribution. The results are a posterior probability distribution that jointly describes the model parameters (e.g., all slope coefficients in a linear regression model). The posterior probability distribution of each parameter is often summarized as a credible interval (CI), which constitutes a direct probability statement about the parameter of interest. Bayesian inference answers the basic question “What is the probability of a hypothesis given our observed data and any prior information we might have?” This is in contrast to frequentist inference, where probability is defined as how often something occurs in the long run (e.g., “If I were to hypothetically replicate a study many times, what is the probability of the observed or more extreme mean catch rates if the new management program is not effective?”). Frequentist inference treats model parameters as fixed, unknown values and treats the data as random. Frequentist inference makes decisions based on how unlikely the observed values are if there is no effect and draws conclusions about the size of the effect from 95% confidence intervals that are based on hypothetical replicates. The 95% confidence intervals tell us, given a hypothetically large number of surveys, how often (95%) our calculated confidence interval would overlap the parameter’s true value (noting that we have no way of knowing whether our calculated 95% confidence interval overlaps the true value or not). This definition effectively renders the use of frequentist probability statements, which only apply to the sampling, useless as a direct measure of probability regarding a specific parameter. For example, we can say with 95% confidence that this sample of fish is not different from the main stock, but we cannot say that there is a 95% probability that this sample of fish is the same as the main stock. Frequentist inference with NHST uses *P*-values to answer the question “What is the probability of observing our data or more extreme data given that some hypothesis (i.e., specified statistical model) is true?”

Why Should I Care about Bayesian Inference?

There are at least two reasons why you might care about Bayesian inference: either (1) you want to be able to better understand and critique articles that use Bayesian methods or (2) you want to incorporate Bayesian methods into your own quantitative toolbox for analyzing data. Bayesian inference is being used at an increasing rate in fisheries management. Since 2000, fisheries-related journals have seen a rise in the number of papers that use Bayesian analyses (based on a topic search conducted during June 2017 in Web of Science; Figure 1). *Transactions of the American Fisheries Society* (TAFS), the *Canadian Journal of Fisheries and Aquatic Sciences* (CJFAS), and *Fisheries Research* (FR) have exhibited the most consistent increasing trend. In 2016, 7 (6.4%, TAFS), 7 (4.5%, CJFAS), and 11 (4.0%, FR) of the published articles in those journals had “Bayesian” in the topical keywords and employed the methodology in their analyses.

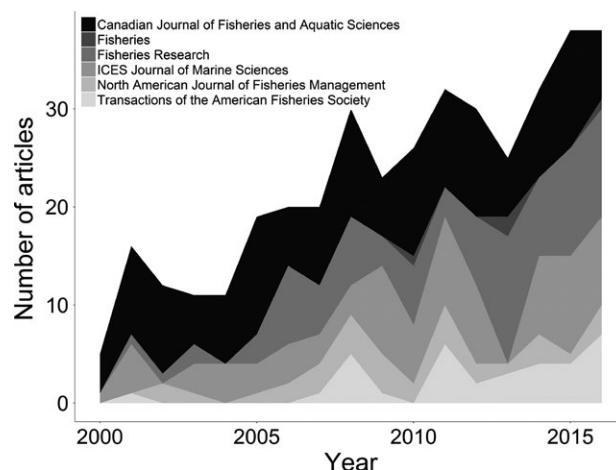


Figure 1. Stacked frequency plot showing the time series of the number of published articles that used Bayesian analysis in fisheries-related journals between 2000 and 2016 (ICES = International Council for the Exploration of the Sea). Journals are grouped by different shades of gray.

Bayesian inference has been gradually gaining momentum over the past few decades because of its many advantages over NHST and *P*-values. Interestingly, there is even a journal—albeit outside of our field (*Basic and Applied Social Psychology*)—that put a blanket ban on NHST and *P*-values in favor of parameter estimation methods including Bayesian inference (Trafimow and Marks 2015). Additionally, the American Statistical Association (ASA) clarified the use and interpretation of *P*-values by releasing a formal policy statement (the only such statement that has been released by the ASA; Wasserstein and Lazar 2016). This statement clarifies that *P*-values are not a measure of probability and do not measure the size of an effect, cautioning that policy decisions should not be made based solely on whether a *P*-value is below some threshold. The ASA policy statement also provides alternatives to *P*-values, such as Bayesian methods, that emphasize estimation over testing. Thus, understanding the general methodology of Bayesian inference and how it is interpreted can help you critique and understand this growing segment of the scientific literature.

There are many advantages to Bayesian inference. Some of the most tangible advantages include (1) improving your ability to draw conclusions conditional on the data (and prior information), (2) easily propagating uncertainty through hierarchical relationships, (3) easily obtaining uncertainty for derived quantities, (4) incorporating latent variables and functions thereof (e.g., hierarchical occupancy models; Royle and Kéry 2007), (5) incorporating prior knowledge, (6) describing more ecologically realistic models, and (7) being able to express your findings in terms of probability that are easier for nonscientists to understand (see Kruschke 2010 for more details on the advantages of Bayesian inference).

What Can Bayesian Inference Do for Me?

Have you ever thought to yourself, “I wish I could tell this group of anglers there is some specific probability that the new management program will increase catch rates”? If you have, Bayesian inference can help you do that! Bayes’ theorem is the only method of analyzing data to produce probabilities of different hypotheses (Gelman et al. 2014). Concluding

probabilities of outcomes based upon different management scenarios has already been widely used in the management of the world's fisheries (methods synthesized by Punt and Hilborn 1997). Two recent examples of applied management studies that have used Bayesian inference include the development of mortality models to assess the outcomes of regulations on Largemouth Bass *Micropterus salmoides* populations and to predict the results of a new size limit on snapping turtle *Chelydra serpentina* harvest (Kerns et al. 2015; Colteaux and Johnson 2017). Bayesian inference has even been used to inform the management of Walleyes (i.e., the target species sought by our favorite wandering Florida fisherman), as Tsehay et al. (2016) estimated the probabilities of spawning stock biomass, harvest, and a population crash through the use of a hierarchical age-structured stock assessment model. In your own work, Bayesian inference can provide outcome probabilities that can better inform management decisions, regardless of the simplicity or complexity of the analysis.

BAYES' THEOREM

Bayesian inference uses probability theory as a formal way of incorporating new data with prior information to make a direct probability statement about a hypothesis: this is the foundation of Bayesian inference and is based on Bayes' theorem (equation 1; Figure 2). According to Bayes' theorem, the posterior probability distribution, $P(\theta|X)$, of model parameters (θ) given observed data (X) is calculated by

$$P(\theta|X) = \frac{P(X|\theta)P(\theta)}{\int P(X|\theta)P(\theta)d\theta}, \quad (1)$$

where $P(X|\theta)$, the likelihood, denotes the probability distribution of the data given the parameters; $P(\theta)$ denotes the prior probability distribution of the model parameters; and the denominator is a normalizing parameter, calculated by summing across all possible parameter values weighted by the strength of belief in those values to scale the results to range between 0 and 1. Thus, the posterior probability distribution equals the probability distribution of the data given the parameters, multiplied by the prior probability distribution

of the model parameters, all divided by the sum across all possible probability distributions of data multiplied by all possible parameter values weighted by the strength of belief in those values. Conventionally, $P(X|\theta)$ is denoted as the likelihood. However, $P(X|\theta)$ is calculated from an assumed sampling distribution that is conditional on the data (X), not on θ . That is, $P(X|\theta)$ is first defined, and after the data (X) are observed, the same function is used and assumed to be proportional to the likelihood such that $L(\theta | X) \propto P(X | \theta)$. For a thorough review of Bayes' theorem, see Carlin and Louis (2008), Gelman et al. (2014), and McElreath (2016).

The posterior probability distribution is used to make all statistical inference and represents all that is known about the parameter after combining the prior probability distribution with new data. All parameters in a model and all derived quantities (e.g., difference between two parameters; see relative weight example below) have a posterior probability distribution. The posterior probability distribution can be summarized by its mean or median, with the spread of the distribution summarized with quantiles. The most common summary of the posterior probability distribution to represent full uncertainty is the 95% CI, which is the range of values that are bounded by the upper 97.5% quantile and lower 2.5% quantile of the probability distribution.

Prior information is arguably the most important and greatest advantage of Bayesian inference. Bayesian inference permits researchers to directly incorporate previous knowledge about model parameters in a transparent and defensible manner. Prior probability distributions measure how plausible all potential parameter values are before we see new data. When priors are based on the literature or on expert opinions, they are considered "informative priors." In contrast, when the researchers have no basis to construct an informative prior distribution, all possible values can be given equal probability and considered "reference priors" or "diffuse priors." When prior probability distributions are based on reference priors, the mean of the posterior probability distributions, particularly with simple models (e.g., linear regression), is similar to the point estimates of frequentist inference. However, drastically different interpretations remain because of the underlying

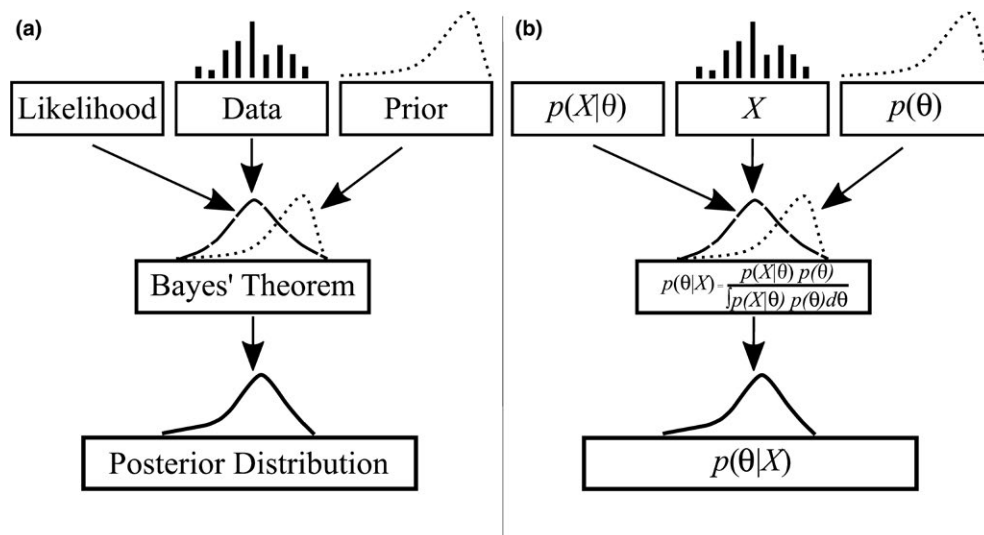


Figure 2. Bayesian inference flow chart using (a) a description and (b) equations (see the Bayes' Theorem section for symbol definitions).

definitions of probability under the different paradigms (see the section What Is Bayesian Inference?). Furthermore, some critics argue that the use of informative priors in model building may be considered subjective (Martin et al. 2012). Indeed, prior distributions and the reliance on these “priors” have been the subject of much debate (Dennis 1996; Huelsenbeck et al. 2002; McCarthy and Masters 2005). Nevertheless, the value of prior information cannot be discounted, and Bayesian inference provides a transparent mechanism for its inclusion (Kuhnert et al. 2010). We would argue that there are very few situations where the researcher would truly have no prior information and that their analyses would benefit from the inclusion of available prior information.

Informative prior probability distributions can be categorized in two ways: “population” and “state of knowledge.” The “population” category includes setting biologically realistic limits on the bounds of a parameter—for example, constraining estimates of detection probability to be between 0 and 1. The “state of knowledge” category includes expert knowledge and published literature. As we demonstrate later in this article, prior information based on the current state of knowledge allows us to make informed decisions where we would otherwise not have biologically relevant parameters (see von Bertalanffy growth model example). Many examples of incorporating informative prior probability distributions in fisheries applications can be found in the stock assessment literature (McAllister and Ianelli 1997; Romakkaniemi 2015). Other ecological applications outside of fisheries include evaluating the impacts of grazing on birds (Martin et al. 2005), estimating mule deer *Odocoileus hemionus* survival and abundance (Lukacs et al. 2009), and estimating poaching mortality of gray wolves *Canis lupus* (Liberg et al. 2011). While incorporating informative prior information can increase the usefulness of your analysis, the prior probability distribution must be carefully selected and must be supported by good science.

Combining the likelihood and prior probability distribution into the posterior probability distribution can generally not be accomplished using standard integral approximation, and there is often no analytic solution. Thus, sampling techniques that calculate numerical approximations of model parameters are required to overcome these issues. Markov-chain Monte Carlo (MCMC) is the most common method of sampling from the posterior probability distribution; other, less-common methods of sampling from the posterior probability distribution include grid search (Kruschke 2015) and sampling-importance resampling (Rubin 1988). A full description of MCMC methods is beyond the scope of this article; thus, we only present a cursory overview here. The MCMC methods include several different algorithms that sample from the posterior distribution with a Markov chain. Constructing a Markov chain is a process that generates a series of random numbers that are dependent on the previous random number and nothing else. Most MCMC processes begin with one set of random numbers that represent parameters in your model. A new set of random numbers is then generated and compared with the first. If the new set of random numbers provides a better fit given the data and prior information, they are saved and then compared to a new set of random numbers. If they do not provide a better fit given the data and prior information, they are not saved and a new set of random numbers is generated and compared to the initial set. This process continues for hundreds and often thousands of iterations until the saved values have converged on the posterior probability distribution. The different algorithms that perform MCMC

differ in their proposals and accepting or rejecting criteria, and there is a variety of methods to identify convergence to the posterior probability distribution. There is also an initial period in the chain, called the “burn-in” period, that is removed because it is unlikely to have come from the posterior distribution. It is also common to “thin” MCMC chains to remove the correlation between successive iterations and reduce the length of the chain and thus the amount of memory required to save the chain. This is accomplished by only saving every i th step in the chain. The number of iterations to discard between saved steps will be dependent on the amount of correlation and the total number of iterations used in the MCMC chain. It is common to set the number of thinning steps to 3, but values greater than 10 are often used for very long chains (e.g., >10,000 iterations). The end result is a series of “iterations” with values for each parameter being estimated or each quantity being derived that represents the joint posterior probability distribution. A more technical description of how MCMC works is provided by Congdon (2007).

APPLIED FISHERIES EXAMPLES

We present two increasingly complex fisheries examples to provide an applied framework using actual data. These examples are common and often first introduced in undergraduate fisheries management courses and in popular fisheries textbooks (Walters and Martell 2004; Isely and Grabowski 2007). Here, we emphasize how the results are interpreted as a probability distribution of credible values as opposed to rejecting or failing to reject a null hypothesis. We also demonstrate the use of prior information to improve inference of a common fisheries model.

When conducting any analysis using Bayesian inference, there are specific details that must be presented in the narrative that describes the methods. These include the software used, the number of concurrent MCMC chains, the total number of iterations, the number of burn-in steps, the number of thinning steps, the number of saved steps, and convergence diagnostics. The most common software programs used when fitting Bayesian models are JAGS (Plummer 2003), BUGS (Lunn et al. 2000), and Stan (Carpenter et al. 2017). All three are incorporated into the R programming environment through downloadable R packages. The specific details for the two examples presented here, with complete model specification with JAGS and R code, are available in the online Supplement. Posterior probability distributions of the parameter estimates are summarized with their medians and 95% CIs. The analyses presented here are not intended to provide a thorough assessment of either fishery. Rather, we use these as example applications of Bayesian inference to common fisheries scenarios.

Comparison of Fish Condition between Years Using Relative Weight (Bayesian t -test)

Relative weight is a common fisheries management metric that is used to monitor the response of a fish population due to regulation changes (Blackwell et al. 2000) and provides a familiar and practical example. Relative weight is the ratio of the weight of an individual fish to a standard weight for a given length, scaled to be between 0 and 100,

$$W_{ri} = \left(\frac{W_i}{W_{si}} \right) \times 100, \quad (2)$$

where W_{ri} is the relative weight of individual fish i , W_i is the weight of individual fish i , and W_{si} is a length-specific standard

weight predicted by the weight–length regression for individual fish i . The specific equation used to calculate W_s comes from the regional species-specific weight–length formula (Neumann et al. 2012),

$$\log_{10}(W_s) = a + b \cdot \log_{10}(\text{TL}), \quad (3)$$

where a is the intercept, b is the slope, and TL is the total length of the individual fish. In this example, we compare W_r values between two groups by using the Bayesian two-sample t -test (Kruschke 2012).

The Bayesian two-sample t -test is simply the comparison of group means and is analogous to the frequentist two-sample t -test. However, the key difference between the two is that the frequentist t -test is only comparing group means to determine whether they are “significantly” different, whereas the Bayesian t -test is comparing the groups’ mean and uncertainty (i.e., SD) to determine a difference and the extent of the difference. The Bayesian two-sample t -test describes the data from both groups with a normal distribution (a t -distribution can be used as an alternative to account for outliers),

$$y_{ki} \sim \text{normal}(\mu_k, \sigma_k), \quad (4)$$

where y_{ki} is the observed W_r for individual i in group k , μ_k is the mean of group k , and σ_k is the SD of group k . Note that the normal distribution in JAGS is parameterized with the mean and precision ($1/\sigma_k^2$). Reference priors are used for μ_k and σ_k :

$$\mu_k \sim \text{normal}(0, 1000) \quad (5)$$

$$\sigma_k \sim \text{uniform}(0, 20). \quad (6)$$

The assumptions for a Bayesian two-sample t -test (comparison between group means) do not change because we are using Bayesian inference (i.e., we assume independent observations and do not assume equal variances).

Application: long-term (1992 versus 2002) comparisons of Yellow Perch relative weight

Notable changes in management regulations and the Lake Michigan ecosystem have occurred over the past 30 years (Madenjian et al. 2002). Within Indiana waters, commercial fishing was closed in 1997 and a daily recreational creel limit of 15 fish was imposed. In addition to this, introductions of invasive species (e.g., zebra mussel *Dreissena polymorpha*, quagga mussel *D. bugensis*, and Round Goby *Neogobius melanostomus*) have altered the Lake Michigan food web (Griffiths et al. 1991; Lauer et al. 2004; Nalepa et al. 2009). The numerous factors affecting Yellow Perch *Perca flavescens* provide an ideal situation to evaluate changes in mean and SD of W_r as an applied example of Bayesian inference. We used a Bayesian two-sample t -test (Kruschke 2012) to determine (1) whether the average and SD of Yellow Perch W_r changed after a 10-year period (1992 and 2002), and (2) if so, how much they changed.

The data used for this analysis were from a long-term monitoring program conducted in southern Lake Michigan. Yellow Perch were sampled at three fixed sites using nighttime bottom trawling at the 5-m depth contour in 1992 and 2002 (other years were available; however, for demonstration purposes, we only use 2 years of data). For more details about the sampling program, see Forsythe et al. (2012). Sites were

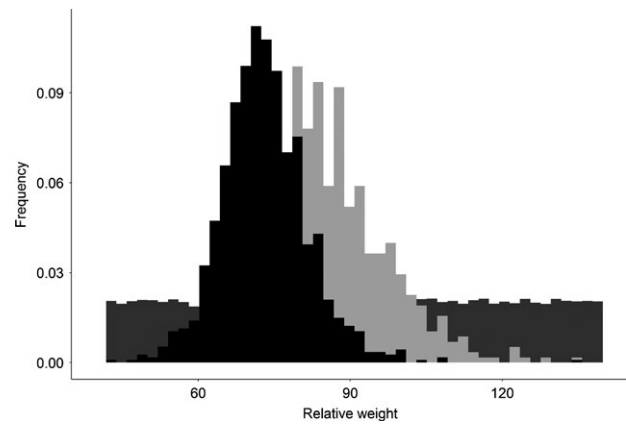


Figure 3. Histograms of data distributions for Yellow Perch relative weight in southern Lake Michigan during 1992 (light gray) and 2002 (black). The dark-gray histogram represents the prior probability distribution of mean relative weight for each group (see Figure 4 for the full prior probability distribution).

sampled twice each month (July and August) for a total effort of 12 h in each year. After each night, a random subsample of 300 Yellow Perch (age ≥ 1) were measured for TL and total weight. Standard weight was calculated using the parameters reported by Neumann et al. (2012).

Overall, 1,701 fish were included in the analysis. Relative weights ranged from 42.2 to 142.4 (Figure 3). Mean W_r was 86.3 (95% CI = 85.4–87.3) in 1992 and was 73.2 (95% CI = 72.7–73.7) in 2002 (Figure 4). The distributions of mean W_r in 1992 and 2002 were clearly different, but one important question the manager will often ask is “How much different are the mean W_r values in 2002 compared to 1992?” This question can easily be answered under the Bayesian approach. In this example, we simply subtracted the posterior probability distribution of the mean W_r for 1992 from that of the mean W_r for 2002. By doing this, we obtained a derived parameter with a measure of uncertainty—a result that is more difficult to obtain under the frequentist paradigm with NHST. The change in W_r corresponded to a decrease in mean W_r of 13.1 (95% CI = 12.2–14.2) from 1992 to 2002. These CI results are interpreted as there being a probability of 0.95 that mean W_r decreased by between 12.2 and 14.2. Estimates of SD were 11.3 (95% CI = 10.7–11.9) for 1992 and 9.1 (95% CI = 8.8–9.5) for 2002, indicating a decrease in variability of 2.2 (95% CI = 1.5–2.9) from 1992 to 2002.

Because of the rich information contained in the results of Bayesian inference, we can begin to ask questions that have direct and meaningful implications for management. As we have discussed, the results represent probability distributions about parameters (e.g., W_r). Thus, the percentage of the posterior probability distribution that is greater than, less than, or between management benchmarks represents the probability of reaching those specific benchmarks. For example, suppose a management benchmark for mean W_r is 73 (or any specific W_r that managers are interested in); if this benchmark is reached, we would conclude that some management action should be taken. To evaluate this scenario, we would calculate the probability that the mean W_r for Yellow Perch in 2002 was 73 or less. This is accomplished by determining the percentage of the posterior probability distribution for the 2002 mean W_r that was less than 73 (total

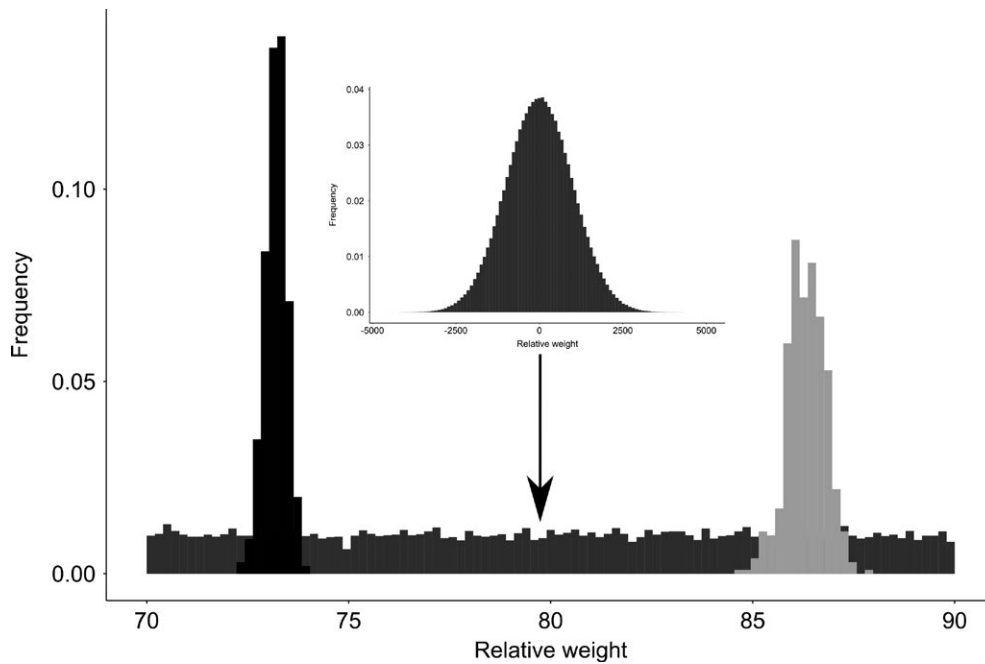


Figure 4. Prior probability distribution (inset dark-gray histogram and the dark-gray histogram in the main figure) and posterior probability distributions of mean relative weight for Yellow Perch sampled from southern Lake Michigan in 1992 (light-gray histogram) and 2002 (black histogram). The prior probability distribution is depicted in the inset to show the full probability distribution, as it appears flat when the x-axis is scaled to show details of the posterior probability distributions.

number of iterations in the posterior probability distribution that were 73 or less divided by the total number of iterations in the posterior probability distribution). In this example, we calculated a probability of 0.51 that the mean W_r in 2002 was less than or equal to 73. The fisheries manager can use this calculated probability to determine whether a new management action should be taken. Similarly, suppose we decide that 73 is too low and that a W_r of 80 or less would warrant some management action. The entire posterior probability distribution for Yellow Perch W_r in 2002 was less than 80; thus, we obtained a probability of 1.00 that W_r was less than 80. Features such as generating the probabilities of achieving management benchmarks make Bayesian methods desirable for use in management decisions.

Evaluating Growth Using the von Bertalanffy Model (Nonlinear Regression)

Understanding how individual organisms change in length over time is one of the fundamental pieces of information used in fisheries management. The change in length over time is typically assessed with length-at-age data acquired from observing annular rings on a given bony structure (e.g., otolith, spine, opercle, etc.). Information on growth is used to predict future yield (Quist et al. 2010) and to set harvest limits (Reed and Davies 1991). To estimate growth rates, a biologist must select a growth model that plausibly reflects the relationship between length and age data. The von Bertalanffy growth model is one of the most common models used to describe organisms' growth (Midway et al. 2015; Hupfeld et al. 2016; Doll et al. 2017; Ogle et al. 2017),

$$y_i = L_{\infty}[1 - e^{-k(\text{age}_i - t_0)}] + \varepsilon_i, \quad (7)$$

$$\varepsilon_i \sim \text{normal}(0, \sigma), \quad (8)$$

where y_i is the length of fish i , L_{∞} is the theoretical maximum mean TL achieved, κ is the Brody growth coefficient (with units t^{-1}), age_i is the age of fish i , t_0 is the theoretical age at zero length, and ε_i is a random error term with a mean of 0 and a standard deviation σ . Note that the normal distribution in JAGS is parameterized with the mean and precision ($1/\sigma^2$).

Application: Monroe Reservoir Walleye age and growth

For this application, we used Bayesian inference with a nonlinear regression model to estimate parameters associated with the von Bertalanffy growth model. We additionally incorporated prior information about model parameters. The data used for this analysis originated from Walleye sampling conducted at Monroe Reservoir (Brown and Monroe counties, Indiana) in October 2011 using 18 overnight sets of experimental-mesh gill nets. Scale samples were taken from all Walleyes for age and growth determination. For more information about the sampling protocol at Monroe Reservoir, see Kittaka (2008).

We estimated parameters by using reference prior probability distributions and also extended the model to incorporate informative prior probability distributions (Table 1). The parameters L_{∞} and κ were estimated on the log scale to restrict them to positive values. Informative prior probability distributions were obtained from existing Walleye records at FishBase.org (Froese and Pauly 2017). We only included records that were from the United States and that had estimates for all parameters (i.e., L_{∞} , κ , and t_0). This resulted in 26 observations for each parameter. Prior probability distributions were specified by taking the arithmetic mean and SD of each parameter. Note that the prior probability distributions for L_{∞} and κ are the mean and SD on the log scale.

Thirty-three Walleyes were included in the analysis. Total lengths ranged from 33 to 64 cm, and ages ranged from 1 to 9 years. Only one age-6 and one age-9 fish were observed. Estimates of L_{∞} were higher with reference prior probability

Table 1. Prior probability distributions used in the von Bertalanffy growth model for Walleyes in Monroe Reservoir, Indiana (L_{∞} = theoretical maximum mean TL achieved; κ = Brody growth coefficient; t_0 = theoretical age at zero length). The normal distribution is parameterized with the mean and precision ($1/\sigma^2$), and the uniform distribution is parameterized with minimum and maximum values. A reference prior for the SD (σ) was used under both conditions.

Parameter	Reference prior probability	Informative prior probability
$\log(L_{\infty})$	<i>Normal</i> (0, 1/1,000)	<i>Normal</i> (4.27, 0.351)
$\log(\kappa)$	<i>Normal</i> (0, 1/1,000)	<i>Normal</i> (-1.16, 0.546)
t_0	<i>Normal</i> (0, 1/1,000)	<i>Normal</i> (-0.47, 0.522)
σ	<i>Uniform</i> (0, 100)	<i>Uniform</i> (0, 100)

distributions, while κ and t_0 estimates were lower with reference prior probability distributions (Table 2; Figure 5). Reference prior probability distributions resulted in greater uncertainty (i.e., wider 95% CI) compared to informative prior probability distributions (Table 2; Figure 5) for all parameters. Incorporating informative prior probability distributions also resulted in increased SDs (Figure 6) to accommodate the data and information in the prior probability distribution.

Looking at the study as a whole, something is very apparent: this Walleye data set contained few older fish, a scenario that is common in routine fisheries surveys. However, through the use of informative prior probability distributions, we can be better prepared to deal with data sets like these. When prior information was not included, the lack of older fish resulted in unrealistic estimates of L_{∞} because the curve did not reach an asymptote (Figure 7), thus limiting practical use of the results. Although Walleyes over 70 cm have been collected, the majority of individuals are typically under 60 cm (Kittaka 2008). Thus, an average L_{∞} greater than 65 cm is not a biologically realistic scenario. Furthermore, our estimate of κ using the reference prior probability distribution resulted in the center of the posterior probability distribution (0.06) being lower than any value reported at FishBase.org for Walleyes in the United States (Table 2; Figure 7). This immediately suggests that without incorporating prior information, our estimate was biased low. Assessing growth information from limited data can often be misleading due to a lack of older fish, and inferences drawn using reference prior probabilities can result in inaccurate conclusions. In this example, the use of informative prior probability distributions resulted in more biologically realistic parameter estimates.

The present Walleye example demonstrates two key aspects of Bayesian inference. The first is the reallocation of belief. Incorporating new data reallocated the probabilistic belief to a new posterior probability distribution with reference and informative priors (Figure 5: compare groups A, B; groups C, D). The second key aspect of Bayesian inference demonstrated in this example is that prior information can be incorporated in the form of a prior probability distribution. The informative prior probability used here is the reason why the posterior probability distribution was more biologically realistic. The biological realism was worked into the model from the beginning by including information from 26 other studies.

Conclusion

Bayesian inference is a powerful and flexible tool that can be useful to all fisheries professionals. Although being able to make direct probabilistic statements about a hypothesis is desirable, perhaps the most advantageous aspect of Bayesian inference is the ability to formally incorporate prior information

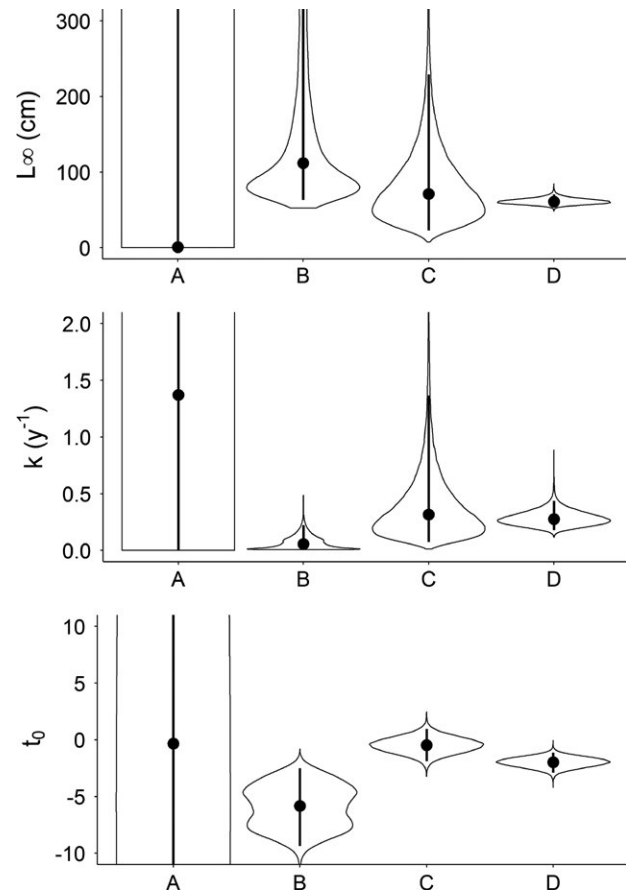


Figure 5. Violin plots of probability distributions for parameters of the von Bertalanffy growth model for Walleyes in Monroe Reservoir, Indiana (L_{∞} = theoretical maximum mean TL achieved; κ = Brody growth coefficient [year^{-1}]; t_0 = theoretical age at zero length). Area within each violin plot represents the probability of parameter values; the widest portion of the violin plot indicates the highest probability. The solid point on each violin plot represents the median of the probability distribution, and the solid line represents the 95% credible interval. Group A is the reference prior probability distribution for each parameter (because of the extreme uncertainty in the prior, it appears flat); group B is the posterior probability distribution based on the reference prior probability distribution for each parameter (see Table 1 for details); and group D is the posterior probability distribution based on the informative prior probability distribution.

Table 2. Posterior probability distributions, reported as the median with lower and upper limits of the 95% credible interval (in parentheses), from the von Bertalanffy growth model for Walleyes in Monroe Reservoir, Indiana, based on reference and informative prior probability distributions (see Table 1; L_{∞} = theoretical maximum mean TL achieved; κ = Brody growth coefficient; t_0 = theoretical age at zero length). Note that L_{∞} (cm) and k (year^{-1}) have been back-transformed to the original scale.

Parameter	Reference prior probability	Informative prior probability
L_{∞}	109 (64, 505)	58 (54, 63)
κ	0.06 (0.01, 0.22)	0.40 (0.31, 0.53)
t_0	-5.75 (-9.24, -2.58)	-1.12 (-1.54, -0.72)
σ	2.83 (2.23, 3.75)	3.33 (2.58, 4.48)

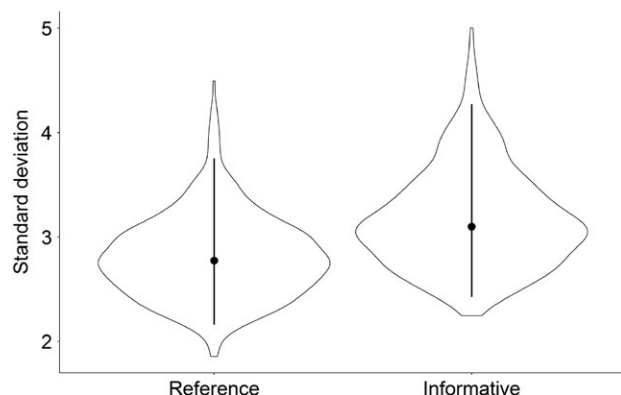


Figure 6. Violin plot depicting the posterior probability distribution of the SD from the von Bertalanffy growth model for Monroe Reservoir Walleyes based on use of either reference or informative prior probability distributions. See Figure 5 for an explanation of violin plot elements.

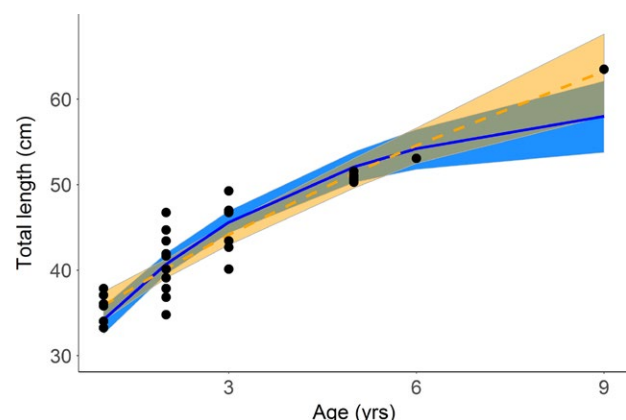


Figure 7. Mean growth curves for Monroe Reservoir Walleyes based on reference (orange) and informative (blue) prior probability distributions. Points represent observed values; the dashed line is the median of the posterior probability distribution with reference prior probability distributions; the solid line is the median of the posterior probability distribution with informative prior probability distributions; and the shaded areas represent the 95% credible regions for the reference (orange) and informative (blue) prior probability distributions.

in a defensible and logical way. Our field has grown substantially in its literature base over the past century, and it seems worthwhile to stand on these past studies as we reach toward new and higher syntheses in the fisheries world. The literature provides a vast library of data that researchers can use to develop informative prior distributions and is already being used in fisheries stock assessments (Punt and Hilborn 1997). There is no reason why we should not incorporate this historical information into our research and management programs. Herein, we have provided one example of how to understand and incorporate prior information into common fisheries models. There are many available sources that provide additional examples and details about how prior information can be incorporated into one's research (Millar 2002; McCarthy and Masters 2005; Kuhnert et al. 2010; Martin et al. 2012).

Our goal with this article is to provide fisheries managers, educators, and students with an introduction to Bayesian inference. This is intended as a first step toward a more complete understanding of what Bayesian inference is, when to use Bayesian

inference, and how to apply Bayesian inference in one's own research. There are many articles and books available to help readers with the most elementary as well as the most advanced steps (Kéry 2010; Parent and Rivot 2013; Gelman et al. 2014; Kruschke 2015).

Bayesian inference is not a panacea and should not be viewed as a "one size fits all" method of analysis. Although many do tend to prefer Bayesian methods, it is necessary to also be pragmatic and view Bayesian inference as another tool to use when needed. Ultimately, of greatest importance is that when a problem is approached, the best statistical method to answer the question at hand is used.

ACKNOWLEDGMENTS

We are grateful for the helpful comments and suggestions provided by Derek Ogle and Sandra Clark-Kolaks on earlier drafts. We thank Jeff Schaeffer, who encouraged the topic for this article, and the anonymous reviewers, who helped to improve it. We thank Aaron Lerner for providing the data on the number of papers published in AFS journals. We also thank Brian Breidert, Sandra Clark-Kolaks, Dave Kittaka, the Indiana Department of Natural Resources, and Ball State University for providing the Yellow Perch data from Lake Michigan and the Walleye age and growth data from Monroe Reservoir. This is Publication 2018-06 of the Quantitative Fisheries Center at Michigan State University.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

REFERENCES

- Blackwell, B. G., M. L. Brown, and D. W. Willis. 2000. Relative weight (W) status and current use in fisheries assessment and management. *Reviews in Fisheries Science* 8(1):1–44.
- Carlin, B. P., and T. A. Louis. 2008. *Bayesian methods for data analysis*, 3rd edition. CRC Press, Taylor & Francis Group, Boca Raton, Florida.
- Carpenter, B., A. Gelman, M. D. Hoffman, D. Lee, B. Goodrich, M. Bentaouat, M. Brubaker, J. Guo, P. Li, and A. Riddell. 2017. Stan: a probabilistic programming language. *Journal of Statistical Software* [online serial] 76(1):696.
- Colteaux, B. C., and D. M. Johnson. 2017. Commercial harvest and export of snapping turtles (*Chelydra serpentina*) in the United States: trends and the efficacy of size limits at reducing harvest. *Journal of Nature Conservation* 35:13–19.
- Congdon, P. 2007. *Applied Bayesian modelling*, 2nd edition. Wiley & Sons Ltd., Chichester, West Sussex, UK.
- De Ridder, D., S. Vanneste, and W. Freeman. 2014. The Bayesian brain: phantom percepts resolve sensory uncertainty. *Neuroscience and Biobehavioral Reviews* 44:4–15.
- Dennis, B. 1996. Should ecologists become Bayesians? *Ecological Applications* 6:1095–1103.
- Doll, J. D., T. E. Lauer, and S. Clark-Kolaks. 2017. Yield-per-recruit modeling of two piscivores in a Midwestern reservoir: a Bayesian approach. *Fisheries Research* 191:200–210.
- Forsythe, P. S., J. C. Doll, and T. E. Lauer. 2012. Abiotic and biotic correlates of Yellow Perch recruitment to age-2 in southern Lake Michigan, 1984–2007. *Fisheries Management and Ecology* 19:389–399.
- Froese, R., and D. Pauly. 2017. FishBase [online database]. Available: www.fishbase.org. (July 2017).
- Gelman, A., J. B. Carlin, H. S. Stern, D. B. Dunson, A. Vehtari, and D. B. Rubin. 2014. *Bayesian data analysis*, 3rd edition. CRC Press, Taylor & Francis Group, Boca Raton, Florida.
- Griffiths, R. W., D. W. Schloesser, J. H. Leach, and W. P. Kovalak. 1991. Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes region. *Canadian Journal of Fisheries and Aquatic Sciences* 48:1381–1388.
- Huelsenbeck, J. P., B. Larget, R. E. Miller, and F. Ronquist. 2002. Potential applications and pitfalls of Bayesian inference in phylogeny. *Systematic Biology* 51:673–688.

- Hupfeld, R. N., Q. E. Phelps, S. J. Tripp, and D. P. Herzog. 2016. Mississippi River basin Paddlefish population dynamics. *Fisheries* 41:600–610.
- Isely, J. J., and T. B. Grabowski. 2007. Age and growth. Pages 187–228 in C. S. Guy and M. L. Brown, editors. *Analysis and interpretation of freshwater fisheries data*. American Fisheries Society, Bethesda, Maryland.
- Jacquemin, S. J., and J. C. Doll. 2014. Body size and geographic range do not explain long term variation in fish populations: a Bayesian phylogenetic approach to testing assembly processes in stream fish assemblages. *PLOS (Public Library of Science) ONE* [online serial] 9(4):e93522.
- Kerns, J. A., M. S. Allen, J. R. Dotson, and J. E. Hightower. 2015. Estimating regional fishing mortality for freshwater systems: a Florida Largemouth Bass example. *North American Journal of Fisheries Management* 35:681–689.
- Kéry, M. 2010. *Introduction to WinBUGS for ecologists*. Elsevier, Burlington, Massachusetts.
- Kittaka, D. S. 2008. Monroe Reservoir, Monroe and Brown Counties, 2007 fish community survey report. Indiana Department of Natural Resources, Fisheries Section, Indianapolis.
- Kruschke, J. K. 2010. What to believe: Bayesian methods for data analysis. *Trends in Cognitive Sciences* 14:293–300.
- Kruschke, J. K. 2012. Bayesian estimation supersedes the *t* test. *Journal of Experimental Psychology: General* 142:573–603.
- Kruschke, J. K. 2015. *Doing Bayesian data analysis: a tutorial with R and BUGS*, 2nd edition. Elsevier, Burlington, Massachusetts.
- Kuhnert, P. M., T. G. Martin, and S. P. Griffiths. 2010. A guide to eliciting and using expert knowledge in Bayesian ecological models. *Ecology Letters* 13:900–914.
- Lauer, T. E., P. J. Allen, and T. S. McComish. 2004. Changes in Mottled Sculpin and Johnny Darter trawl catches after the appearance of Round Gobies in the Indiana waters of Lake Michigan. *Transactions of the American Fisheries Society* 133:185–189.
- Liberg, O., G. Chapron, P. Wabakken, H. C. Pedersen, N. T. Hobbs, and H. Sand. 2011. Shoot, shovel, and shut up: cryptic poaching slows restoration of a large carnivore in Europe. *Proceedings of the Royal Society B* 279:910–915.
- Lukacs, P. M., G. C. White, B. E. Watkins, R. H. Hahn, B. A. Banulis, D. J. Banulis, D. J. Finley, A. A. Holland, J. A. Martens, and J. Vayhinger. 2009. Separating components of variation in survival of mule deer in Colorado. *Journal of Wildlife Management* 73:817–826.
- Lunn, D. J., A. Thomas, N. Best, and D. Spiegelhalter. 2000. WinBUGS—a Bayesian modeling framework: concepts, structure, and extensibility. *Statistics and Computing* 10:325–337.
- Madenjian, C. P., G. L. Fahnenstiel, T. H. Johengen, T. F. Nalepa, H. A. Vanderploeg, G. W. Fleischer, P. J. Schneeberger, D. M. Benjamin, E. B. Smith, J. R. Bence, E. S. Rutherford, D. S. Lavis, D. M. Robertson, D. J. Jude, and M. P. Eberner. 2002. Dynamics of the Lake Michigan food web, 1970–2000. *Canadian Journal of Fisheries and Aquatic Sciences* 59:736–753.
- Martin, T. G., M. A. Burgman, F. Fidler, P. M. Kuhnert, S. Low-Choy, M. McBride, and K. Mengersen. 2012. Eliciting expert knowledge in conservation science. *Conservation Biology* 26:29–38.
- Martin, T. G., P. M. Kuhnert, K. Mengersen, and H. P. Possingham. 2005. The power of expert opinion in ecological models using Bayesian methods: impact of grazing on birds. *Ecological Applications* 15:266–280.
- McAllister, M. D., and J. N. Ianelli. 1997. Bayesian stock assessment using catch–age data and the sampling-importance resampling algorithm. *Canadian Journal of Fisheries and Aquatic Sciences* 54:284–300.
- McCarthy, M. S., and P. Masters. 2005. Profiting from prior information in Bayesian analysis of ecological data. *Journal of Applied Ecology* 42:1012–1019.
- McElreath, R. 2016. *Statistical rethinking: a Bayesian course with examples in R and Stan*. CRC Press, Taylor & Francis Group, Boca Raton, Florida.
- McGrayne, S. B. 2012. *The theory that would not die: how Bayes' rule cracked the Enigma code, hunted down Russian submarines, and emerged triumphant from two centuries of controversy*. Yale University Press, New Haven, Connecticut.
- Midway, S. R., T. Wagner, S. A. Arnett, P. Biondo, F. Martinez-Andrade, and T. F. Wadsworth. 2015. Spatial and temporal variability in growth of Southern Flounder (*Paralichthys lethostigma*). *Fisheries Research* 167:323–332.
- Millar, R. B. 2002. Reference priors for Bayesian fisheries models. *Canadian Journal of Fisheries and Aquatic Sciences* 59:1492–1502.
- Nalepa, T. F., D. L. Fanslow, and G. A. Lang. 2009. Transformation of the offshore benthic community in Lake Michigan: recent shift from the native amphipod *Diporeia* spp. to the invasive mussel *Dreissena rostriformis bugensis*. *Freshwater Biology* 54:466–479.
- Neumann, R. M., C. S. Guy, and D. W. Willis. 2012. Length, weight, and associated indices. Pages 637–676 in A. V. Zale, D. L. Parrish, and D. W. Willis, editors. *Fisheries techniques*, 3rd edition. American Fisheries Society, Bethesda, Maryland.
- Ogle, D. H., T. O. Brenden, and J. L. McCormick. 2017. Growth estimation: growth models and statistical inference. Pages 265–353 in M. C. Quist and D. Isermann, editors. *Age and growth of fishes: principles and techniques*. American Fisheries Society, Bethesda, Maryland.
- Parent, É., and É. Rivot. 2013. *Introduction to hierarchical Bayesian modeling for ecological data*. Chapman & Hall, CRC Press, Boca Raton, Florida.
- Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In K. Hornik, F. Leisch, and A. Zeileis, editors. *Proceedings of the 3rd international workshop on distributed statistical computing*. Available: <https://www.r-project.org/conferences/DSC-2003/Proceedings>. (February 2018).
- Punt, A. E., and R. Hilborn. 1997. Fisheries stock assessment and decision analysis: the Bayesian approach. *Reviews in Fish Biology and Fisheries* 1997(7):35–63.
- Quist, M. C., J. L. Stephen, S. T. Lynott, J. M. Goeckler, and R. D. Schultz. 2010. Exploitation of Walleye in a Great Plains reservoir: harvest patterns and management scenarios. *Fisheries Management and Ecology* 17:522–531.
- Rahikainen, M., I. Helle, P. Haapasaari, S. Oinonen, S. Kuikka, J. Vanhatalo, S. Mäntyniemi, and K. Hoviniemi. 2014. Towards integrative management advice of water quality, oil spills, and fishery in the Gulf of Finland: a Bayesian approach. *Ambio* 43:115–123.
- Reed, J. R., and W. D. Davies. 1991. Population dynamics of Black Crappies and White Crappies in Weiss Reservoir, Alabama: implications for the implementation of harvest restrictions. *North American Journal of Fisheries Management* 11:598–603.
- Romakkaniemi, A., editor. 2015. Best practices for the provision of prior information for Bayesian stock assessment. ICES (International Council for the Exploration of the Sea) Cooperative Research Report 328.
- Royle, J. A., and M. Kéry. 2007. A Bayesian state-space formulation of dynamic occupancy models. *Ecology* 8:1813–1823.
- Rubin, D. B. 1988. Using the SIR algorithm to simulate posterior distributions. Pages 395–402 in J. M. Bernardo, M. H. DeGroot, D. V. Lindley, and A. F. M. Smith, editors. *Bayesian statistics*, 3rd edition. Oxford University Press, Cambridge, Massachusetts.
- Trafimow, D., and M. Marks. 2015. Editorial. *Basic and Applied Social Psychology* 37:1–2.
- Tsehay, I., B. M. Roth, and G. G. Sass. 2016. Exploring optimal Walleye exploitation rates for northern Wisconsin Ceded Territory lakes using a hierarchical Bayesian age-structured model. *Canadian Journal of Fisheries and Aquatic Sciences* 73:1413–1433.
- Walters, C. J., and S. J. D. Martell. 2004. *Fisheries ecology and management*. Princeton University Press, Princeton, New Jersey.
- Wasserstein, R. L., and N. A. Lazar. 2016. The ASA's statement on *p*-values: context, process, and purpose. *American Statistician* 70:129–133. 