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Discriminating alternative stock–recruitment models and evaluating uncertainty in model structure

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Abstract

Fish stock–recruitment (S–R) assessment is one of the most essential keystones for fisheries management. Yet the analysis involves a variety of uncertainties. Amidst these difficulties, uncertainty in model structure is perhaps the most problematical to investigate because no rigorous statistical techniques can be used to explore the fundamental biological processes in S–R relationships. In this paper, I used computer simulations to investigate: (1) the differences between the estimated parameters of alternative S–R models as a function of stock characteristics: population growth rate, data range, fishing mortality, and process noise; and (2) the probability of selecting a correct model using information criteria. Two popular S–R functions, the Ricker and the Beverton–Holt models, were used as examples. Time series data were generated from a known S–R model and fitted by alternative models. The results show that when the two models fit the data similarly well, significant differences in parameters existed between the alternative models. The Ricker model tended to underestimate the population growth rate (initial slope) and the carrying capacity parameter, whereas the Beverton–Holt model overestimated these parameters. The management quantities (e.g., optimal virgin stock size) produced by one model were more conservative (i.e., larger optimal stock size or lower optimal harvest rate) under some conditions but became less conservative under other conditions. The differences between the alternative models were functions of the population growth rate, long-term fishing mortality, and data range of the stock size. The correct and incorrect models were statistically indistinguishable. For typical fishery data the probability of selecting the correct model based on information criteria was approximately 0.70 for the Ricker model and 0.61 for the Beverton–Holt model.

Keywords: Stock–recruitment; Model uncertainty; Ricker; Beverton–Holt

1. Introduction

Fish stock–recruitment (S–R) analysis is among the most important assessments of fish population dynamics. Generally, fisheries scientists believe that there is a fundamental relationship between spawner abundance and subsequent recruitment (Myers and Barrowman, 1996). Because of its importance in fishery management, a great deal of effort has been devoted to studies of S–R relationships (Hilborn and Walters, 1992; Quinn and Deriso, 1999; Haddon, 2001). Many fishery management reference points and policies are based on such a relationship (Kimura, 1988; Clark, 1991; Myers et al., 1994; Bradford et al., 2000; Brodziak, 2002). For example, escapement goals for many Pacific salmon stocks are established based on S–R analysis (CTC, 1999). Scientists routinely conduct stock assessments for a variety of ground fish species to develop annual harvest guidelines and rebuilding plans for stocks along the West Coast of the continental United States (PFMC, 2002; Ralston, 2002). Several mathematical models have been built to describe the relationship between spawning stock and recruitment at various life stages. These models include Beverton and Holt (1957), Ricker (1954), Cushing (1971, 1973), Deriso (1980), Schnute (1985), Shepherd (1982), Gamma (Reish et al., 1985), and recently the hockey-stick models (Barrowman and Myer, 2000; Bradford et al., 2000).

Fishery research and management includes a variety of uncertainties, ranging from a lack of basic data to institutional inefficiency (Rice and Richards, 1996; Francis and Shotton, 1997; Flaaten et al., 1998; Weeks and Berkeley, 2000). There are at least three major uncertainties involved in S–R modeling: process noise, measurement error, and model uncertainty (Charles, 1998; Schnute and Richards, 2001). The first two types of uncertainties have been extensively studied (Ludwig

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and Walters, 1981; Walters and Ludwig, 1981; Hilborn and Walters, 1992; Ehrhardt and Legault, 1997; Quinn and Deriso, 1999; Valpine and Hastings, 2002). These two types of uncertainties can be quantitatively captured and evaluated by modern statistical methods. The third uncertainty, model uncertainty, is also called structural uncertainty or model misspecification. This uncertainty reflects a fundamental lack of knowledge about underlying fish biological processes. There are two basic types of model uncertainties. First, the assumed structural relationships between variables may be incorrect. Second, potentially influential relationships and dynamics may have been totally excluded from the model (Mace and Sissenwine, 2002). Because quantitative techniques cannot deal with model uncertainties, this topic is particularly challenging to fishery researchers. The appropriate form of the S–R relationship remains a significant issue of debate for many stocks (Patterson et al., 2001). Kimura (1988) showed that the particular family of S–R curves that is used can strongly affect the conclusions of a stock assessment. Levels of exploitation that appear near optimum under one family of recruitment curves may force a stock to extinction under another.

The literature on S–R relationships is substantial. However, we lack a systematic evaluation of the differences in the estimated parameters from different models. Fisheries management often depends on these estimated parameters and if alternative models produce inconsistent results the impact on management decisions could be profound. A typical S–R model is a mathematical equation in which recruitment is a function of spawner abundance. Most models were originally based on certain biological assumptions (Ricker, 1954; Beverton and Holt, 1957). However, scientists commonly fit a mathematical equation to observed stock size and recruitment data and estimate the parameters in the equation without considering the validity of the underlying biological assumptions. In practice, any mathematical model may be used for spawner–recruitment relationships as long as it goes through the origin, increases monotonically at low spawning levels, and shows some level of density dependence at high spawning levels (Quinn and Deriso, 1999). We may not understand the underlying biological processes in S–R relationships, or the relationships may be too complex to be described with a simple mathematical function. Statistical criteria, rather than biological considerations, have become the primary arbitrator to determine which model is suited for a particular species. This dependence on statistical fit could be misleading, particularly if the better fit of one model over others is spurious because of measurement and process error.

While some scientists continue to recommend using statistical criteria for selecting a best S–R model, others consider statistical criteria to be potentially misleading. Alternative models may fit a data set equally well and yet produce very different parameter estimates. For example, when investigating different models to estimate the threshold biomass required to ensure protection of recruitment, Myers et al. (1994) found dramatically different results for the Ricker model versus the Beverton–Holt model, even though the goodness-of-fit was rarely different (Barrowman and Myer, 2000). However, empirical analysis of 72 real datasets from a variety of fish stocks using the Ricker and Beverton–Holt models resulted in a mixed picture on which S–R model was more conservative (Myers et al., 1994). When comparing spawner–recruitment curves for coho salmon, Barrowman and Myer (2000) concluded that the Beverton–Holt model always overestimated the initial slope and carrying capacity. In an extensive simulation study that compared biological reference points, Williams and Shertzer (2003) concluded that very different biological reference points emerged from the Beverton–Holt and Ricker functions. They found that with typical stock–recruitment data it was very difficult to determine which function best represented the behavior of a particular stock, although they recommended that the Beverton–Holt function was a better choice for management because of its more conservative biological reference point values. Wang and Liu (2006) compared two criteria that may be used to select among S–R functions and found that both Akaike information criterion (AIC) and Bayesian information criterion (BIC) were valid. However, in another simulation study, Valpine and Hastings (2002) found that the Ricker model systematically fit the data better than the Beverton–Holt model even when the latter was used as the underlying model to generate the data. They cautioned that using information criteria (such as AIC) can be misleading. These inconsistent results can cause disagreement over which models should be used for a particular stock or management decision (Patterson, 1999; Hammond and O'Brien, 2001).

The objectives of this paper were two-fold. It is possible that one model may be more conservative than other models under certain circumstances. Therefore, the first objective was to systematically compare the differences between the estimated parameters from alternative S–R models under a variety of scenarios. This objective relied on selecting a time series dataset that could be fit by two or more competing models equally well. The second objective was to test whether the correct and incorrect models were statistically distinguishable. The correct model referred to the one that best represented the underlying function that produced S–R relationship, whereas the incorrect model was the alternative one. I used an approach reported in the literature of simulating a series of data from a known S–R function and then fitting alternative models to these data. Of the models mentioned above, the classical Beverton–Holt and Ricker models are most popularly used in fisheries research. Therefore, I chose to investigate these two models and compare their results. Obviously, other models could also be examined by this method. Both models have two parameters to be estimated. The Ricker model assumes, biologically, that the mortality rate of the recruitment is proportional to the stock abundance (Ricker, 1954, Hilborn and Walters, 1992). Consequentially, the curve is dome-shaped with a declining limb at high spawner abundance. In contrast, the Beverton–Holt model is based on the assumption that the mortality rate of the recruitment is linearly dependent upon the number of fish alive in the cohort at any time. As a result the curve is asymptotic in shape (Beverton and Holt, 1957; Hilborn and Walters, 1992). In this paper, spawner abundance or stock size refers to either the number of spawners, biomass, or index of either, while recruitment or production refers to the number, biomass, or index of offspring. This study is primarily pertinent to semelparous species such as Pacific salmon, but it should also