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Temporally varying natural mortality: Sensitivity of a virtual population analysis and an exploration of alternatives

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ABSTRACT

Cohort reconstructions (CR) currently applied in Pacific salmon management estimate temporally variant exploitation, maturation, and juvenile natural mortality rates but require an assumed (typically invariant) adult natural mortality rate (d_A), resulting in unknown biases in the remaining vital rates. We explored the sensitivity of CR results to misspecification of the mean and/or variability of d_A, as well as the potential to estimate d_A directly using models that assumed separable year and age/cohort effects on vital rates (separable cohort reconstruction, SCR). For CR, given the commonly assumed $d_A = 0.2$, the error (RMSE) in estimated vital rates is generally small (≤ 0.05) when annual values of d_A are low to moderate (≤ 0.4). The greatest absolute errors are in maturation rates, with large relative error in the juvenile survival rate. The ability of CR estimates to track temporal trends in the juvenile natural mortality rate is adequate (Pearson's correlation coefficient > 0.75) except for high d_A (≥ 0.6) and high variability (CV > 0.35). The alternative SCR models allowing estimation of time-varying d_A by assuming additive effects in natural mortality, fishing mortality, and/or maturation rates did not outperform CR across all simulated scenarios, and are less accurate when additivity assumptions are violated. Nevertheless an SCR model assuming additive effects on fishing and natural (juvenile and adult) mortality rates led to nearly unbiased estimates of all quantities estimated using CR, along with borderline acceptable estimates of the mean d_A under multiple sets of conditions conducive to CR. Adding an assumption of additive effects on the maturation rates allowed nearly unbiased estimates of the mean d_A as well. The SCR models performed slightly better than CR when the vital rates covaried as assumed. These separable models could serve as a partial check on the validity of CR assumptions about the adult natural mortality rate, or even a preferred alternative if there is strong reason to believe the vital rates, including juvenile and adult natural mortality rates, covary strongly across years or age classes as assumed.

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1. Introduction

Fisheries stock assessments use a variety of statistical and mathematical tools in an attempt to understand the current abundance and dynamics of fished stocks. While the form of model employed in a stock assessment may vary considerably depending on scientific and management context, estimates of natural morality are an integral component of stock assessment. It is known that many results from stock assessments can be heavily influenced by the choice of natural mortality (e.g., biological reference points, Goodyear, 1993). Yet, owing to the difficulty of directly estimating natural mortality, fixed external estimates or assumed values are frequently used. Temporal and/or age-dependent variation in natural mortality undoubtedly exists and the assumption of fixed natural mortality likely results in assessment errors. However, estimation of temporal variation in natural mortality in stock assessments is rare (Brodziak et al., 2011). While this is a topic of ongoing research and progress is being made (e.g., Hollowed et al., 2000;

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Lee et al., 2011; Deroba and Schueller, 2013), challenges remain (e.g., Maunder and Wong, 2011; Francis, 2012) and incorporation of time-varying mortality into stock assessments has been slow and largely limited to a few taxa (Deroba and Schueller, 2013).

Cohort reconstructions or virtual population analyses (Hilborn and Walters, 1992) performed on tagged cohorts of salmon are the backbone of salmon stock assessment (e.g., Mohr, 2006; O'Farrell et al., 2012; PSC CTC, 2014). Reconstruction of cohorts from coded wire tag recovery data (Nandor et al., 2010) allows estimation of age-specific abundance, harvest rates, maturation rates, and other vital rates used for salmon management. An assumption of known, and typically invariant, natural mortality rates for adult salmon is required for statistical identifiability when using current techniques that treat cohorts independently (Hankin et al., 2005). Unfortunately, this means that vital rate estimates are biased to an unknown extent by assumed and arbitrary values assigned to adult natural mortality rates. For example, a real increase in the natural mortality rate between age 2 and age 3 in a particular year could be erroneously interpreted instead as unusually high maturation at age 2 and low early life survival for the corresponding cohort.

Biased vital rates are an obvious problem for management models. In addition, such biases may impair ecological or evolutionary insights when cohort reconstruction results are used, for example, to explore putative drivers of variation in maturation rates (e.g., Hankin and Logan, 2010) or juvenile survival (Sharma et al., 2013; Kilduff et al., 2014). In addition, it is of course impossible to explore the role of environmental conditions or predators (Hilborn et al., 2012) in driving variation in adult natural mortality if such mortality is *a priori* assumed to be constant.

This paper therefore has two major goals. First, we use simulation studies to thoroughly explore the sensitivity of results from traditional cohort reconstructions assuming known, temporally invariant adult natural mortality to misspecification of mean mortality rates and to variability in mortality rates. Second, we explore the potential for direct estimation of time-varying adult natural mortality rates for a range of biological scenarios. The existing literature on salmon population dynamics uses the terms "rate", "fraction", "probability", and "proportion" in ways that are not always consistent. Unless we make specific reference to instantaneous rates when referring to other studies, the word "rate" is used throughout this paper, along with a unitless number, to represent the conditional probability or proportion of fish making a specified transition over one time step of the model. This is consistent with use of the term "rate" in cohort reconstruction models used by the Pacific Salmon Commission (e.g., PSC CTC, 2014) and Pacific Fishery Management Council (e.g., O'Farrell et al., 2012).

2. Methods

Virtual population analysis (or cohort analysis) is applied to catch-at-age data to back calculate the number of individuals alive prior to a mortality event, with the goal of obtaining abundance estimates and mortality rates (e.g., Fry, 1949; Pope, 1972). This method requires a known terminal fishing mortality rate for the maximum age and specified natural mortality rates. Classical analyses of this type are deterministic in that the stochastic variation inherent in the data is not accounted for, and the accompanying model is fully saturated (no degrees of freedom); thus measures of statistical uncertainty are not readily available (Megrey, 1989).

A model resembling the classical virtual population analysis of Pope (1972) is applied to the management of Pacific salmon stocks (e.g., Mohr, 2006; O'Farrell et al., 2012; PSC CTC, 2014). This model, termed cohort reconstruction, employs a monthly rather than annual time step, but similar to Pope (1972), a pulse fishery occurs at the start of each time step followed by natural mortality (Xiao and Wang, 2007). For the cohort reconstruction, the final time step in each year includes an additional mortality event, maturation, and a terminal maturation rate of 1.0 is required as opposed to a specified terminal fishing mortality rate. Additionally, cohort reconstruction methods estimate monthly or annual, rather than instantaneous, mortality rates and include an accounting for incidental fishing mortality.

Since the monthly models simply apportion a constant annual natural mortality rate across months, and depend on detailed month-specific harvest data and assumed mortality of discards, we chose an annual model for tractability, interpretability, and faster simulation. We did not explicitly model incidental fishing mortality, assuming it was incorporated into catch estimates. This cohort reconstruction (CR, abbreviations are defined in Table 1) assumes an annual sequence of discrete mortality events: ocean fishery mortality followed by maturation followed by ocean natural mortality. (Fish that mature return to the river where they are either caught in river fisheries or spawn and die shortly thereafter.) This reconstruction, in common with similar methods, requires a fixed age 2, 3, and 4 ("adult") natural mortality rate specified *a priori*. It is equivalent to Pope's (1972) cohort analysis when catch also includes escapement and fish are instantaneously removed from the population at the beginning of the year (Xiao and Wang, 2007).

We develop our example based on a subset of the data available on cohorts of hatchery-reared salmon tagged in distinct release groups using a coded wire tag (Nandor et al., 2010), specifically yearling releases of Klamath River fall Chinook salmon produced at Iron Gate Hatchery, California. We assume that a single cohort of age 1 coded wire tagged fish is released annually, that these fish are not subject to the ocean fishery or maturation at age 1, and that fish live a maximum of five years (all age 5 fish that survive the ocean fishery mature). Fish age increments by one year following

Table 1
Abbreviations used and their definition.

Abbreviation	Definition
IGH	Iron Gate Hatchery
ME	Mean error
RMSE	Root mean square error
MPE	Mean percent error
MAPE	Mean absolute percent error
CR	Cohort reconstruction
SCR	Separable cohort reconstruction
SCR-1	SCR model variant 1: Rates on complementary log-log scale: fishing mortality separable (age + year); maturation non-separable (age * cohort) for age 2 and 3, constant for age 4; natural mortality non-separable (age-class * year).
SCR-2	SCR model variant 2: Rates on complementary log-log scale: fishing mortality separable (age + year); maturation separable (age + cohort) for age 2 and 3, constant for age 4; natural mortality non-separable (age-class * year).
SCR-3	SCR model variant 3: Rates on complementary log-log scale: fishing mortality separable (age + year); maturation non-separable (age * cohort) for age 2 and 3, constant for age 4; natural mortality separable (age-class + year).
SCR-4	SCR model variant 4: Rates on complementary log-log scale: fishing mortality separable (age + year); maturation separable (age + cohort) for age 2 and 3, constant for age 4; natural mortality separable (age-class + year).
Con.2	Constant generating rates with an adult natural mortality rate of 0.2.
Var.2	Time varying generating rates with an adult natural mortality rate mean value of 0.2.
Var.4	Time varying generating rates with an adult natural mortality rate mean value of 0.4.
Add.2	Time varying generating rates with additive year and age or cohort and age effects on the complementary log-log scale and an adult natural mortality rate mean value of 0.22.