Part IV. Determining Escapement Goals to Rebuild Wild Steelhead Populations: What Role Should Stock Recruit Analysis Have?

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Introduction

Bill McMillan's historical analysis of Olympic Peninsula and other wild winter steelhead populations in western Washington provides important evidence that most wild winter-run steelhead populations in Washington State are depressed when compared to conservative estimates of population numbers in the decades immediately preceding 1960. Significantly, the depression in the abundance of major populations in large river basins in Puget Sound, such as the Skagit, and on the Olympic Peninsula, such as the Hoh, appears to be well out of proportion to the known or estimated loss of spawning and rearing habitats in these systems. In such circumstances population abundance data from recent decades, principally spawner and recruit data, will be of little use in determining escapement goals, if the long-term preservation of these populations requires rebuilding to the kinds of abundance and diversity that existed in the not-so-distant past. What guidance if any can traditional stock-recruit analysis provide in these circumstances?

To answer this question, I first present a basic description of stock-recruit analysis applied to steelhead and discuss both the strengths and the weaknesses of this kind of population analysis. Along the way I will make clear the problems with the concept of "maximum sustained yield" (MSY) as a reference point for setting escapement goals. Population analysis in the real world is inevitably fraught with uncertainties which increase the risk involved in following a course of action derived from the analysis. Consequently, it is critical than any population analysis not only recognize and acknowledge the uncertainties attending the analysis but also properly propagate the uncertainties through the analysis and display them in the results in a way that can inform a risk assessment of alternative courses of action. It will be argued that stock-recruit analysis, properly performed, can be of use when employed in this way. It will be seen that this is a much more limited (though more honest) use of stock-recruit analysis than is the norm in fisheries management. Along the way it will also be shown that concepts like MSY fall by the wayside.

Age Structure, Overlapping Generations and Density Dependence

Steelhead populations are composed of individuals of several different age and size categories or classes. Age and size as well as individual growth rates are closely related to maturity. Populations can be broadly sub-divided into mature (adult) and immature (juvenile) members. Depending upon specific population conditions, either or both adults and juveniles may be composed of several ages classes. Individuals may become mature at age 3, 4, 5 or more, and may remain juveniles for 2, 3, 4, or more years.

Most steelhead populations, therefore, contain a mixture of juveniles and adults of differing ages in differing proportions. For most populations, this results in the offspring from any one year's spawning (called a *cohort*) maturing at different ages over a period of several years. For example, if the adult component of a particular population in any one year contains 3, 4 and 5 year-olds, members of the year 2001 cohort will make up part of the spawning populations in 2004, 2005, and 2006. Conversely, the spawning population in year 2001 will be made up of members of the 1996, 1997, and 1998 cohorts. In addition, steelhead are *iteroparous*. They do not experience programmed death after spawning as Pacific salmon do and are, therefore, capable of spawning more than once. Many coastal wild steelhead populations throughout the Pacific Rim, including Washington State, exhibit repeat spawning rates as great or greater than ten percent (Pavlov et al. 2001, WDFW 2006). So, in any given year the spawning population will include individuals that have contributed offspring to the population in the recent past and individuals that are contributing for the first time.

In this way, steelhead populations are composed of individuals of different ages from several different generations. Such populations are characterized by *age structure* and by an *overlapping of generations*. Both are important features of the life history of each population.

A third concept often employed in characterizing populations of steelhead and other salmonids is *density dependence*. This is the notion that the survival of members of a population between key life stages, such as from one-year-old parr to two-year-old smolt, is in part dependent upon the size of the population relative to the size (and quality) of its habitat. At relatively high densities, a smaller proportion of individuals can survive than when densities are lower. Density dependence is generally thought to be an important feature of juvenile steelhead survival in the freshwater environment. (The ocean survival rate for adults is not thought to be density dependent — the survival rate for 4-year-old steelhead is the same whether there are 5,000 or 500,000.)

Stock-Recruit Relationships

When it comes to characterizing steelhead and salmon populations and managing them for harvest, age structure, overlapping generations and density dependence are reflected in what are known as *stock-recruit relationships* -- mathematical relationships that are believed to appropriately characterize the fundamental biological process(es) governing the relationship between parents (spawners) and progeny (recruits). These relationships are generally depicted by the use of stock-recruit curves, which provide a graphic representation of the underlying mathematical relationship. A stock-recruit curve expresses the number of recruits from a cohort that are expected to be produced by a given number of parent spawners. This is the number of recruits that is predicted to result from a given number of parent spawners under average environmental conditions if the chosen mathematical relationship is the correct one. A recruit is generally defined as an adult of a certain age or life stage available for harvest or spawning. In some contexts, however, it may be more appropriate to focus on recruits at other life stages, such as smolts at the time of outmigration.

Because each year's return (run) is composed of adults of several ages, annual run sizes are usually inadequate predictors of run size in specific future years. Rather, the dynamics of populations like steelhead are better characterized in terms of recruits from annual spawner numbers. This requires decomposing annual run numbers into recruits from the different prior spawning years, based on the age composition of the adult population.

Stock-recruit analysis consists of taking spawning and return data for a series of years, estimating the adult recruitment from each spawning year (using population age and repeat spawner data) and then estimating a spawner-to-recruit function from the series of spawner and recruit data. The estimated function is in the form of a mathematical equation. The equations most commonly employed embody general assumptions about the nature of density dependence experienced by the stock. Two stock-recruit equations are most commonly employed in analyses of salmonid populations, the Ricker and the Beverton-Holt. Both are very similar, so for purposes of illustration in what follows we use the Ricker equation and its associated Ricker curve.[1] The appropriate equation is given in Figure 1. Figure 2 shows a plot of both the Ricker and Beverton-Holt curves for common parameters explained later in this paper.

Stock-recruit equations characterize the dynamics of the population by estimating two variables or "parameters". One parameter (**a or 'alpha'**) characterizes the inherent productivity of the stock at low densities. The other parameter (**b or 'beta'**) determines directly or indirectly the maximum level of recruitment and the spawning stock size at which that level of recruitment is achieved. In combination, the two parameters determine the equilibrium size of the stock (**eq**.), which is the point at which the total spawning escapement produces just enough total recruits to equal and hence to replace itself. This is depicted on the right-most portion of the stock recruit curve by the point at which the curve intersects the straight "replacement" line depicting X# spawners = X# recruits (see Figures 1 and 2).

The curve depicted in Figure 1 indicates the presence of density dependence in the dynamics of this population in two ways: 1) the gradual flattening of the slope of the curve as points on the curve get closer to the apex of the curve and 2) the decline of the curve to the right of the apex. The gradual flattening of the curve as the apex is approached from the left indicates that the addition of specific numbers of spawners to a previous number of spawners results in the addition of proportionately fewer recruits to the total number of recruits. For example, 2000 spawners are predicted to produce over 7000 recruits; but 4000 spawners are expected to produce only 11,000, and 6,000 spawners are expected to produce just over 13,000. Each

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[1] It should be noted, however, that the choice of the stock-recruit model itself is not trivial and can have significant consequences for the estimation of management reference points in particular instances.

additional block of 2,000 spawners adds fewer recruits to the total number of recruits than was added by the preceding block of 2,000.

At the very apex of the curve, the last spawner added to the previous total number of spawners fails to add a single additional recruit. This is the point of maximum recruitment, Rmax, and the number of spawners that produces this recruitment is Smax. After this point is reached, additional numbers of spawners actually lead to fewer total recruits; the number of recruits produced by each additional spawner becomes negative. (The Beverton-Holt equation/curve differs in this respect from the Ricker. Instead of reaching a maximum and then slowly declining, the curvature of the B-H curve keeps decreasing but remains positive and eventually effectively levels off parallel to the horizontal (x) axis, usually to the right of the replacement line. This can be seen in Figure 2.) Finally, at the point of equilibrium at the far right of the curve, where the curve intersects the straight replacement line, the total number of spawners produces just enough total recruitment to replace itself (total #spawners = total #recruits).

Maximum Sustainable Yield

Now, suppose that a population exhibits recruitment dynamics that reflect density dependence of the kind depicted in a stock-recruit curves. What proportion of the annual return can safely be killed (harvested)? If the assumption is made that the curve depicts an underlying long-term biological relationship between spawning numbers and recruitment, there then appears to be a single attractive level of harvest indicated by the curve.

Very simply, there will be one point on the curve at which the difference between the number of recruits produced by a given number of spawners and that number of spawners is greatest. This is the underlying intuition behind the concept known as maximum sustainable yield (MSY).

If we pick any point on the horizontal axis (i.e., any particular number of spawners) and draw a straight vertical line up to the curve, that portion of the vertical line lying above the straight replacement line is the harvestable fraction of the total recruitment that would be produced by that number of spawners. The one unique point on the horizontal axis for which this fraction is greatest is the MSY point. Other points may produce greater numbers of total recruits than the MSY point does, but none of these will provide as great a number in excess of the number of spawners needed to perpetually produce that total recruitment.

MSY seeks to take a constant maximum surplus from the stock annually available for harvest, and to allow to escape to spawn the minimum number that is believed necessary to produce that maximum harvestable surplus. *If* all environmental and life-history conditions pertaining to the stock are constant (average) and remain so over the long run in the face of the additional mortality due to harvest, the successful implementation of MSY will result in a perpetual motion machine in which the annual spawning escapement is always the minimum necessary to produce the maximum harvestable surplus, and that surplus will always be harvested consistently and on an annual basis. Since the assumption is that MSY harvest leaves enough stock for spawning to perpetuate this regime, theoretically, no long-term biological harm occurs, by definition.

It is worth pointing out at this juncture that stock-recruit equations and curves, and associated reference points such as MSY are all about averages – long-term average environmental conditions and average, long-term biological characteristics of populations such as average age composition, and average adult body size, including average female fecundity (number of eggs deposited and fertilized). Real populations, however, are composed of individuals whose biological characteristics vary considerably from one another within and between years. So, not only is there a population average to characteristics such as age-at maturity, size-at-age, and probability of surviving to spawn a second (or third or fourth) time, there is a population variance (both within and between years) to these. This variability itself may be important to the diversity of the population and its ultimate productivity and viability, and may require a special accounting in order to determine a sustainable management reference point beyond the simple estimates arrived at by employing average relationships.

Fitting Stock-Recruit Curves to Spawner-Recruit Data

Spawner-recruit equations (such as the Ricker equation) are "fit" to data sets consisting of time series of annual spawner and recruit numbers, where the annual recruits are reconstructed from the annual abundance of adults returning one or more years in the future depending on the age-structure of the adult population. The fit is typically determined by employing a least-squares regression which minimizes the sum of the squared residual errors between each spawner-recruit data point and the data point predicted by the equation. Figure 1 is typical of most reasonably "good" fits of two-parameter (**alpha** and **beta**) stock-recruit equations in that most of the data points do not lie on the curve. The amount of residual error (lack of fit) is indicated visually by the vertical distances between the predicted value (the point on the curve) and the actual data point. Good fits typically account for 45% to 60% of the total variation in recruitment evident in data sets consisting of consecutive years of data spanning three or more generations (~15 or more years for most steelhead populations).

Residual error results from two broadly distinct sources. The first source includes factors that result in a poor fit of the chosen model (the equation) to the data. This includes factors such as choice of an inappropriate model for the stock-recruit relationship, error in fitting the model to the data, uncertainty in the estimation of parameter values (parameter uncertainty) and measurement error in the data itself. The second source is the natural variation in the stock-recruitment process itself (process variation). If it can be safely assumed that there are no errors in the fit due to factors of the first kind, the residual error indicates the average amount of variation around the average (fitted) curve. So a "good" fit of an appropriate stock-recruit model provides estimates not only of the average productivity and capacity of the stock but the average amount of variability in the recruitment level that is to be expected at each spawning stock size in the data set.

Fundamental Assumptions in Using Stock-Recruit Analysis to Determine Population Management Targets

There are several key assumptions involved in fitting a stock-recruit equation to a particular data set consisting of spawner and recruit numbers and consequently there are a number of fundamental assumptions that underlie the employment of stock-recruit equations for population management purposes. Among the more important assumptions are the following. First, fitting requires assuming that the data themselves are both reasonably accurate and have been obtained using the same procedures (weir counts for example) over the time period of the data set, so that inaccuracies or biases in sampling methods are likely to be consistent (of similar magnitudes and in the same direction of over- or under-estimation of the true numbers) over the time series. Second, fitting requires assuming that the variability in the recruitment process itself (which is the fundamental process that is being modeled) is stable and follows a normal or log-normal distribution. The technical term for this is that the time series being modeled is stationary. To say that the time series is stationary means that while the variation in the number of recruits that can be expected from a given number of spawners is random (and, therefore, to some extent unpredictable) it follows a stable pattern or distribution.

This is in contrast to a time series in which the nature of the variation (the statistical distribution of the variation) is changing. If this is the case, then the stock-recruit analysis cannot be used to determine average biological reference points for managing the stock because the analysis will not be estimating population parameters displayed under stationary conditions. However, the outcome of a stock-recruit analysis can be examined to determine whether this critical assumption is violated. This is done by examining the residuals from the fit of the stock-recruit equation to the actual data points. The residuals are the differences between the actual data points and the number of recruits predicted by the best fit equation for each of the actual spawner numbers. If the residuals (or the logarithms of the residuals) are plotted against time (brood year) there should be a random pattern if the environmentally driven variation in the recruitment process is stationary, as appears to be the case in Figure 3. If the residuals change in magnitude (from positive to negative or vice versa) with time, there is strong evidence that the recruitment process is not stationary, as appears to be the case in Figure 4.

A particularly important feature of the data when species with complex adult age structures are involved is the age structure used to reconstruct the recruits from each brood year. The most appropriate procedure is to sample the actual age structure (including the proportion of repeat spawners) of each annual adult recruit class (from catch and/or spawning ground surveys, for example) and use that year-specific age composition to assign recruits from each return year to the appropriate spawner- (brood-) year class. This is rarely done in practice due to constraints of time, personnel, and/or budget, and perhaps a failure to appreciate its significance.[2] The alternative that is usually resorted to is to obtained an average adult age composition (including proportions of repeat spawners in each age class if this data is available) from a subsample of return years and apply that average age composition to reconstruct recruits for all return years in the data set. This procedure assumes either that the age composition of returning adults does not exhibit significant variation between years or that such inter-annual variation will not significantly affect the estimation of the parameters of the stock-recruit relationship. A recent analysis by Zabel and Levin demonstrated that both of these assumptions are wrong, even when the average age composition is well estimated from the sample data (Zabel and Levin 2002). The significance of this error is discussed later in this article.

Further assumptions are involved in using the results of a particular stock-recruit fitting exercise to determine management targets, such as escapement goals, harvest rates, or rebuilding targets for depressed populations. Most important, assuming that the time series is stationary, it must be assumed that the data series is a) of sufficient length and b) spans a sufficient range of spawner abundance levels to permit a robust estimate of the key parameters and of the environmentally driven variation in the recruitment process. If the process variation is stationary it still may exhibit a temporal pattern (due for example to patterns of climate variation such as rainfall). The data series must be long enough to exhibit this pattern in order to achieve a proper estimate of parameter values. Since most climatic variation affecting salmonid recruitment processes exhibits patterning at decadal and longer intervals, it is nearly impossible to achieve robust estimates of stock-recruit parameters with fewer than 20 years of data. This problem is exacerbated by the fact that the recruitment process itself is inherently autocorrelated because current abundance is the result of recruitment from spawner years in the recent past. The autocorrelation in the data series arising naturally from this feature of the process must therefore be distinguished from the correlation that results from the correlation in environmental phenomena that affect recruitment.

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[2] The data for Quilleute wild winter steelhead provided by WDFW and discussed in this article is an exception in this regard. The composition of the annual returning adult run, including the proportions of repeat spawners in

In order to achieve robust, unbiased estimates of the alpha and beta parameters the data series should ideally capture the natural range of variability in population sizes and environmental dynamics. For instance, the data set should span a range of spawning population sizes from dangerously low to near or above the carrying capacity (unfished equilibrium stock size). This range should be spanned at several levels of the range of variation of environmental variables. Ideally, and apart from genuine conservation concerns regarding very low spawning population sizes, several data points at low spawner numbers are required in order to estimate the alpha parameter of stock-recruit equations. When data points in this range are limited in number (or missing entirely) the fitting procedures commonly used to estimate the parameters will result in the left side of the stock-recruit curve rising sharply until the curve starts to encounter the first left-most real data points, resulting in an exaggeration of the value of alpha and therefore making it appear that the stock is more productive at low spawner numbers than it may be.[3] This may result in over-estimating the resilience of the stock to over-fishing. If the lowest data points in the data set happen to coincide with the more favorable range of the (stationary) environmental variation the effect of this exaggeration would be enhanced (that is, the estimate of alpha will not be informed by recruitment data for low spawning numbers under adverse environmental conditions). This tendency to over-estimate the alpha parameter and under-estimate the beta will be exacerbated by the use of average instead of year-specific age structure to reconstruct recruits, particularly when the return age is dominated by more than one age class (cf. Zabel and Levin, 2001).

When data points at relatively high levels of spawner abundance are missing it is difficult for fitting procedures to estimate the capacity of the stock. Several data points (over the range of environmental variation) at or above the unfished equilibrium size of the stock are required in order to achieve a robust estimate of the equilibrium level. This is also important in order to determine the shape of the stock-recruit relationship itself, and hence to determine the most appropriate stock-recruit equation to fit to the data!

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each age class is estimated from samples from the tribal and recreational angler catch.

This can be seen in Figure 2 which compares Ricker and Beverton-Holt stock-recruit curves with common alpha parameters and common equilibrium stock sizes. The Ricker curve is identical to the curve shown in Figure 1. The beta parameter of the Beverton-Holt curve has been adjusted to produce the same equilibrium value as the Ricker fit. If the Beverton-Holt relationship more appropriately describes the true dynamics of the population, spawner escapements greater than the equilibrium number do not result in depression of the number of recruits, whereas if the Ricker is the better description, such depression in recruitment is to be expected (density dependence is much stronger when spawner numbers are in this range). On the other hand, at lower spawner abundances recruitment levels are lower than when Ricker dynamics obtain -- density dependence manifests itself sooner and the productivity of the stock is estimated to be lower than when the Ricker-like dynamics obtain.

Another feature of standard stock-recruit equations such as the Ricker and the Beverton-Holt that warrants caution when weak data sets are involved are the negative correlations between the alpha and beta parameters (and consequently between the alpha parameter and the equilibrium populations size). When the data are not strongly informative, there will be several pairs of alpha and beta values that fit the data more or less equally well. But among these pairs, the pair with the highest alpha value will have the lowest beta and equilibrium value; conversely, the pair with the largest beta or equilibrium value will have the lowest alpha value. Management reference points, such as MSY, however, will differ significantly among these pairs of candidate fits. This is particularly important when such data sets are from depressed stocks and is discussed further in the next section.

Variation in the Survival of Juvenile Salmonids in the Ocean and Using Smolts as Recruits

Variability in recruitment due to variation in ocean conditions is now widely known to be considerable (see for example, Beamish et al. 1997, Beamish et al. 1999, Beamish et al. 2004a, Beamish et al. 2004b, Mantua et al 1997, Meuter et al 2002). Variation in marine conditions affect the survival of smolts during the first summer and winter in the ocean. This variation can

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[3] This feature is the norm in most steelhead and salmon spawner/recruit data sets with which the author is familiar, even for stocks that are of conservation concern.

be considerable. Smolt-to-adult recruitment rates for Wind River summer steelhead, for example, can vary tenfold between years (Dan Rawding, comment at the 2006 Bi-Annual West Coast Steelhead Managers' Meeting, Port Townsend, Washington, March 7 – 9, 2006).

This variation is density independent and will considerably confound stock recruit analysis that is based upon adults. A given number of adult spawners under similar conditions in the freshwater environment in different years may produce widely different numbers of adult recruits due to different rates of survival of smolts following ocean entry. Conversely, two different levels of abundance in spawners in different years may result in similar levels of adult recruitment due to different marine survival rates of smolts. Such differences in recruitment to adulthood will not be due to any differences in density dependent factors, yet stock-recruit analysis will attribute such differences to density-dependence.

The best way to deal with this problem is to estimate annual outmigrant smolt abundance and treat outmigrant smolts are recruits and to separately monitor smolt-to-adult recruitment for each smolt age-class. Stock-recruit relations between spawners and smolts would then be estimated. Since steelhead populations commonly exhibit two or more smolt ages it is also necessary to sample the age-distribution of the annual smolt outmigration in order to correctly attribute smolts to spawning year. Since density dependence manifests itself in the freshwater segment of juvenile life history and stock-recruit analysis aims to estimate density dependent survival as a function of spawner abundance, this approach makes biological sense particularly from a conservation perspective.[4]

Estimates Derived from Data from Exploited Populations

To summarize the discussion to this point, fitting stock-recruit equations to spawner and recruit data involves the following assumptions and/or requirements:

- the environment during the time period spanned by the data exhibits stationary variation

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[4] Adopting this approach would require a significant investment in smolt monitoring in most Washington steelhead rivers, but the benefits in terms of improved management and improved understanding of wild steelhead population dynamics would likely be considerable.

- the data collection process has minimum measurement error and has been acquired using the same methods during the period or changes in data collection methods over the period are known so that proper adjustments can be made to data acquired earlier in the period with (presumably) less accurate methods
- the correct year-specific age structure has been employed in assigning recruits to brood years or the employment of an average age structure based upon a sample of year-specific age data has been evaluated and shown to produce negligible bias in the resulting estimates of model form and model parameters
- the data series is of sufficient length to encompass the full range of environmental variation affecting the recruitment process with which the stock has evolved and at least three generations of the target species
- the data series includes spawner abundances spanning a broad range of absolute spawner abundances, from relatively low numbers to relatively high numbers exceeding reasonable estimates of spawner capacity and including a range of states of the environment (favorable to unfavorable) for spawner abundances in the low, moderate, and high ranges.

If one or more of these requirements is not satisfied the estimates of model form and model parameters will be likely to contain significant, even considerable, uncertainty. Such uncertainty itself poses risks to the population that may be subjected to management policies derived from the stock-recruit analysis.

There is an additional assumption to the use of stock-recruit analysis to provide targets or guidelines for population management that is perhaps implicit in the assumption of time series stationarity, but worth making explicit at this point:

- the condition of the population that is revealed by the outcome of the stock-recruit analysis reflects the full productive potential of the current population.

This is undoubtedly an assumption underlying MSY harvest management. But it is also operative when stock-recruit analysis is employed to determine harvest rates or escapement goals for conservation purposes.

This assumption in particular should be called into question when the spawner-recruit data comes from an exploited population, one affected by either or both periods of intensive harvest and interactions with hatchery populations. Both of these circumstances apply to wild winter-run steelhead in Washington State. In this section I focus only on the effect of harvest at MSY levels in order to focus on the most salient features of the problem.

When harvest morality is applied to a previously unexploited population it can be expected to impose selective pressures on the population that may cause changes in the age structure of the population and in related life history parameters such as fecundity and sex ratio. In addition, populations in large rivers (6th order and larger) like the Quilleute, the Hoh, or the Skagit are composed of subpopulations that spawn or rear in different tributaries and different sections of large mainstem rivers. Each of these subpopulations likely differ in their productivity and in the capacity of their habitats. These will be affected in different ways by harvest mortality. Some for example will be adapted to extreme conditions that may have relatively high egg and juvenile mortality rates compared to the stocks in the more benign environments of the river basin. These sub-populations will, for example, generally have lower growth rates than the other sub-stocks; they are in this sense "less productive" stocks. But they will nonetheless still be the only extant stock capable of colonizing the more extreme habitats/conditions within the river basin and will, therefore, be important components of the population’s biological diversity.

Each sub-population will have made adaptations to its freshwater spawning and rearing habitats in terms of their age structure, age-at-maturity, individual growth rates, and fertility/fecundity rates that will differ from those of other sub-stocks within the basin. The differences between sub-stocks with regard to these features may be subtle in many cases, but there is good reason to believe that each sub-stock has spent its evolutionary life-time continually adjusting these age-related aspects of its population structure to the dynamics of its environment in a way that optimizes the sub-stock's long-term prospects for survival.

Imagine an MSY harvest and escapement regime being imposed on such a pristine aggregate stock. The stock has a distribution of ages-at-maturity for each sex (including frequency of repeat spawning in the case of steelhead), a distribution of juvenile survival rates, a distribution of smolt ages and associated growth rates, and a distribution of adult mortality rates. All of these aspects of the population structure of this particular aggregate stock are expressed, as it were, in the distribution of sizes, ages, and sexes of adult fish entering the river each year.

Let's attach some run size numbers to this thought exercise by assuming that the Quilleute wild winter steelhead stock during brood years 1978 – 1999 characterized by the stock-recruit curve in Figure 1 is such a pristine stock. This stock would have an annual run/spawning population size of between 11,000 and 20,000 fish. The equilibrium spawning stock size, at which the average number of spawners that produces just enough recruits to replace itself, is somewhere in the neighborhood of 14,000. Natural, principally environmental, variability in survival across all ages and life-stages produces this range in the actual annual run size.

The structure of this population displays a schedule of mortalities across the life histories of the various component stocks organized so as to keep the stock fluctuating around the equilibrium point. Most importantly for the harvest discussion, the stock's life-history characteristics are adjusted so as to achieve and maintain a balance between juvenile and adult mortality rates, fecundities and maturation schedules. Whatever the actual rates are for the survival of age-3 adults to age-4, age-4 to age-5, age-5 to age-6, etc., the stock is adapted and adjusted throughout its life histories so as to maintain itself within the equilibrium range of spawning run sizes.

What is the MSY harvest rate for such a pristine stock? Based on Figure 1, it is 53 percent. MSY escapement is just over 5,700, with an expected recruitment of just under 12,200, resulting in an MSY harvest of 6,400.

Note, however, that we only know what this MSY harvest rate is because we are assuming that we already know that Figure 1 is the correct curve for this stock. But if the stock is truly pristine -- in undisturbed habitat and completely unfished — we have no data upon which to base an estimate for the stock-recruit function. We only get that data by fishing the stock at different levels for over several years or decades and monitoring the resulting annual run and spawning population sizes.

To initiate this MSY escapement regime, the average pristine equilibrium stock size of 14,000 must be harvested down to 5,700. Until the stock is re-adjusted to its new equilibrium spawning escapement regime, 8,300 fish must be harvested annually, a harvest rate of 59 percent; to make the following discussion a bit easier to follow, let’s round this harvest rate to an even 60%.

Think what an additional annual mortality rate of 60 percent on mature adults means to the population. If the average natural mortality rate for adults between age 4 and age 5 is 20 percent, then of every 1000 4-year olds in the ocean, 200 die, leaving 80 percent or 800 to return to spawn as 5-year olds (assuming that age 5 is the oldest adult age in the population). If 60 percent of these 800 are harvested, 320 remain to spawn. From the population's point of view this is identical to the situation in which only 32 percent of 4-year olds survive to spawn as 5-year olds. Compared to the unfished 20 percent mortality, 80 percent survival, the effective mortality rate is 68 percent, the effective survival rate 32 percent. The adult mortality rate between ages 4 and 5 has increased from 20 percent to 68 percent.

What might such an increase in the adult mortality rate do? One thing that we know that it does is select for a younger adult population, and an earlier average age of maturity. Populations that mature earlier tend to grow faster; they have higher annual population growth rates. But, corresponding to this higher growth rate, earlier-maturing populations tend to be smaller in total population size because they are able to occupy only optimal habitats. They are less capable of filling a variety of environmental niches than older, slower-growing, more diverse populations. They are composed of fewer generations, so that each annual returning population (run) represents a higher fraction of the total freshwater-plus-ocean-residing population than a slower growing population composed of more generations and are, therefore, more likely to be dominated by one or two age classes. Another thing is also likely to have happened along the way that further distorts matters: the remaining aggregate stock may have become more productive at low densities than the original population due to the imposition of high harvest rates on the pristine stock. The sub-stocks best able to deal with the imposition of additional, harvest-related mortality are those most productive ones occupying the most productive habitat niches. The less productive stocks that are helping the entire aggregate stock to fill all possible habitat spaces are likely to be the first to be lost.

This combination of life-history adjustments and loss of less productive subpopulations will result in the surviving population having a reduced capacity and an increased productivity when viewed in the aggregate by the time that spawner and recruit data have been acquired. This will be the case even if no detrimental changes in freshwater habitat have occurred. As a result, the stock-recruit curve that is based upon a decade or so of data from a stock that has been heavily fished for two or more generations will likely both under-estimate the potential of the size of the aggregate stock and will over-estimate its inherent productivity — the productivity that occurs at relatively low population densities. Any inadequacy in the data series itself (poor representation of the range of spawner and recruit abundance, short number of data points, and so forth) will reinforce this by tending to produce overestimation of the value of alpha and underestimation of the unfished equilibrium level. Both combine to suggest via the stock-recruit curve that the stock can sustain a low level of spawning escapement, compared to pristine conditions, which will produce a relatively high level of recruitment — as measured solely by the relative size of the difference between the excess of recruitment over the escapement level of the parent stock and that parent stock escapement level itself.

Stock-Recruit Analysis and Population Conservation: Incorporating Uncertainty in Model Estimates

What role then can stock-recruit analysis play in helping to direct management of depressed populations? The combination of past harvest impacts, impacts from hatchery practices, and habitat alteration have variously resulted in the majority of Washington's wild winter-run steelhead populations being depressed to one degree or another. *Spawner and recruit data sets for these populations all suffer defects due to the violation of one or more of the requirements for achieving robust analyses noted in the opening paragraph of the preceding section*. All data sets with spawner data from reasonably well-designed procedures for estimating spawner abundance have no data for brood years prior to the mid-1970s and few (only one to this author's knowledge; see footnote 2 above) reconstruct recruits from annual samples of age-structure. Moreover, all such data was acquired after both the significant increase in hatchery steelhead releases that occurred starting in the mid-1960s and after wild populations had been subjected to a variety of in-river harvest impacts. Equally significant, this period also coincided with further declines in levels of abundance of spawning populations of Pacific salmon, reducing the annual influx of marine-derived nutrients that subsidize secondary production in Pacific Northwest rivers, potentially contributing to reductions in the capacity and/or productivity of freshwater rearing environments.

For all of the several kinds of reasons discussed in this article even the best of stock-recruit data sets for these populations will likely be inadequate for representing the true potential of these populations under bone fide conditions of population recovery, and most resulting model and parameter estimates are likely to under-estimate the real capacity of recovered populations, and consequently will underestimate the minimal levels of abundance required to achieve recovery. The analysis of wild steelhead populations in Puget Sound and the Olympic Peninsula by Bill McMillan supports this contention in a striking way.

There remains a limited use of stock-recruit analysis of the best of these data sets from a conservation management point of view. There are two ways in which stock-recruit analysis can be applied to assist in determining management targets for conserving and rebuilding depressed steelhead populations. Stock-recruit analysis can be used to *identify non-stationarity in the time series which in the case of declines in apparent productivity or capacity can help to alert managers to the need for conservation management*. Stock-recruit analysis can also be used to *estimate provisional abundance targets by properly incorporating parameter uncertainty and process variation* in the analysis and examining the estimates of the equilibrium population size under current conditions.

Even reasonably good data sets with 20 or more consecutive years of data will most likely display uncertainty in parameter estimates as a result of real process variation reflected in the data and the imprecision with which parameter values can be estimated from a finite sample of data. In turn, this uncertainty may also produce uncertainty with regard to which stock-recruit model best represents the basic dynamics of the populations. It is critical that this uncertainty be properly displayed and propagated in inferences as to appropriate management targets.

The best way to represent the uncertainties inherent in these kinds of analyses is by representing the uncertainties as *probability distributions* of the estimated parameters. This requires employing Bayesian methods of statistical inference as the basis for the analysis. Bayesian statistical inference conditions the inference about the parameter values of the model on the data and on *prior distributions* of values of the fundamental model parameters that incorporate all that is known and not known about the likely probability distribution of parameter values. When little biologically relevant information about possible parameter values exists *uninformative prior distributions*, such as the uniform distribution, are employed that give more or less equal weight to parameter values within a broad range within which the true values of the unknown parameter can be expected to lie. Where information exists that can be used to constrain the distribution of values of the unknown parameters *informative prior distributions* reflecting such information can be employed. In either case, the resulting inference yields a true probability distribution of values of the unknown parameters of interest. This distribution is commonly termed the *posterior distribution* because it comes after considering the data.

It light of much of the preceding discussion, there is a greater danger that a stock-recruit analysis will over-estimate the alpha parameter and under-estimate the beta parameter and the equilibrium level of abundance of the current population than that it will underestimate alpha or over-estimate capacity (equilibrium abundance). *From, a conservation perspective, managers should therefore pay more attention to the posterior distribution of the beta parameter and the equilibrium abundance level than to the distribution of alpha*.

As an illustration, Figures 5 - 8 show the posterior distributions of alpha, beta, the residual standard deviation (sigma), and the equilibrium abundance (eq.), from a Bayesian analysis of the data in Figure 1 in which five million random combinations of alpha, beta, and sigma (the residual error) drawn from the prior distributions were evaluated and weighted by their joint likelihoods using the Ricker model. The posterior distribution of equilibrium abundance was calculated directly from the joint posterior distribution of alpha and beta using the relationship eq = Ln(alpha)*beta. The prior distributions were all uniform (uninformative) distributions that each spanned a broad range of biologically reasonable values for each of the three model parameters (alpha, beta, and sigma). The ranges are listed in the headings for Figures 5 – 8.

Figure 9 shows the left cumulative posterior distribution of equilibrium abundance, which is the proportion of the posterior distribution with values less than or equal to the value on the X-axis. The 95th percentile value occurs at approximately 16,000, which means that – conditional on the data, the model (the Ricker equation), and the prior distributions – there is a 5 percent probability that the equilibrium abundance is at least as great as 16,000.

The distributions of alpha, beta, sigma, and the equilibrium abundance are unimodal and moderately well-defined. The posterior distribution of sigma in particular is very narrow and within the range in which environmentally driven variation in recruitment in salmonids is frequently found (0.2 to 0.5), indicating that the data are reasonably informative and the model reasonable. The coefficient of variation (standard deviation/mean) of alpha, beta, and sigma range from 0.175 (sigma) to 0.202 (beta). The coefficient of variation of equilibrium abundance, however, is much smaller (0.077), reflecting the negative correlation between alpha and beta (= -0.877), and indicating the data under the model provide more information about the equilibrium abundance than about either alpha or beta alone.

Given the tendency for estimates of alpha to be inflated when data points at low spawner abundances are lacking as well as the tendency for past exploitation to produce stocks that appear more productive than the historical, unfished stock, managers should be cautious, and perhaps outright skeptical, about high values of alpha (values greater than 4). Further, in view of the negative correlation between alpha and beta and between alpha and equilibrium abundance (= -0.511 in the present case), more attention should be paid to the right end of the posterior distribution of equilibrium abundance to derive provisional management targets for conservation and rebuilding purposes. In the case exemplified in Figures 5 – 9, an escapement management goal in the vicinity of 16,000 would be not be unreasonable.

In view of the reasons for believing that most current wild steelhead populations may be depressed well out of proportion to freshwater habitat damage that has occurred since the mid-1960s (as suggested by McMillan’s analysis of the Hoh wild winter-run steelhead population, for example) and in view of the reasons for believing that past harvest impacts on the steelhead populations themselves (and interactions with hatchery fish and loss of salmon populations) may render current populations smaller in size and less able to take full advantage of extant habitat diversity than they were prior to these impacts, population rebuilding programs should aim to create the conditions that increase the likelihood that increased population diversity is selected. *This requires very low harvest rates and escapement levels that perpetually probe the current capacity of freshwater habitats.*

Spawner-recruit data can be a valuable part of monitoring programs for a high escapement-target based population conservation and rebuilding strategy. In this context, spawner-recruit data that focuses on outmigrant smolts as recruits would be particularly valuable because they would more directly monitor the productivity and capacity of freshwater habitat and their response to all management actions by eliminating variability in marine survival that confounds the analysis of spawner to adult recruit data and by more directly reflecting conditions in freshwater.

When stocks are depressed relative to historic abundances there is little place for MSY management. As shown previously, MSY harvest rates on pristine populations with complex life histories like steelhead are likely to impose selective mortality pressures that result in populations with reduced capacity and higher apparent productivity than the original unfished stock. As a population continues to decline due other factors such as habitat degradation and loss, MSY harvest rates will follow the population down as it declines further in capacity as measured by current stock-recruit data. This data then becomes part of the shifted baseline McMillan (following Pauly 1995) has so eloquently described. Imposition of an MSY harvest rate calculated from the fit of a stock-recruit equation to current spawner and recruit data will keep the population from experiencing selection pressures that favor increased diversity. Such a management strategy will likely increase the extinction risk and prevent the recovery of Washington's depressed wild steelhead populations. *A more robust and ecologically sound strategy for choosing provisional escapement and rebuilding target population levels should employ a liberal estimate of the equilibrium abundance level, chosen from the right end of the probability distribution of equilibrium abundance levels estimated from stock-recruit analyses incorporating all significant sources of uncertainty*.

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FIGURES

Figure 1.

Quilleute Steelhead, Brood Years 1978-1999 (Return Years 1982/83-2004/05) Ricker Equation (R = a*S*EXP^(-S/b), where R is Adult recruits, S is parent generation spawners, and EXP is the base of the natural logarithm, ~2.71828).

a = 3.59; b = 10856; eq = 13875 Rmax = 14,349 (Smax = b = 10856); Smsy = 5730; Rmsy = 12134; Hmsy = 6404; HRmsy = 0.528. The MSY point on the curve is indicated by the red triangle.

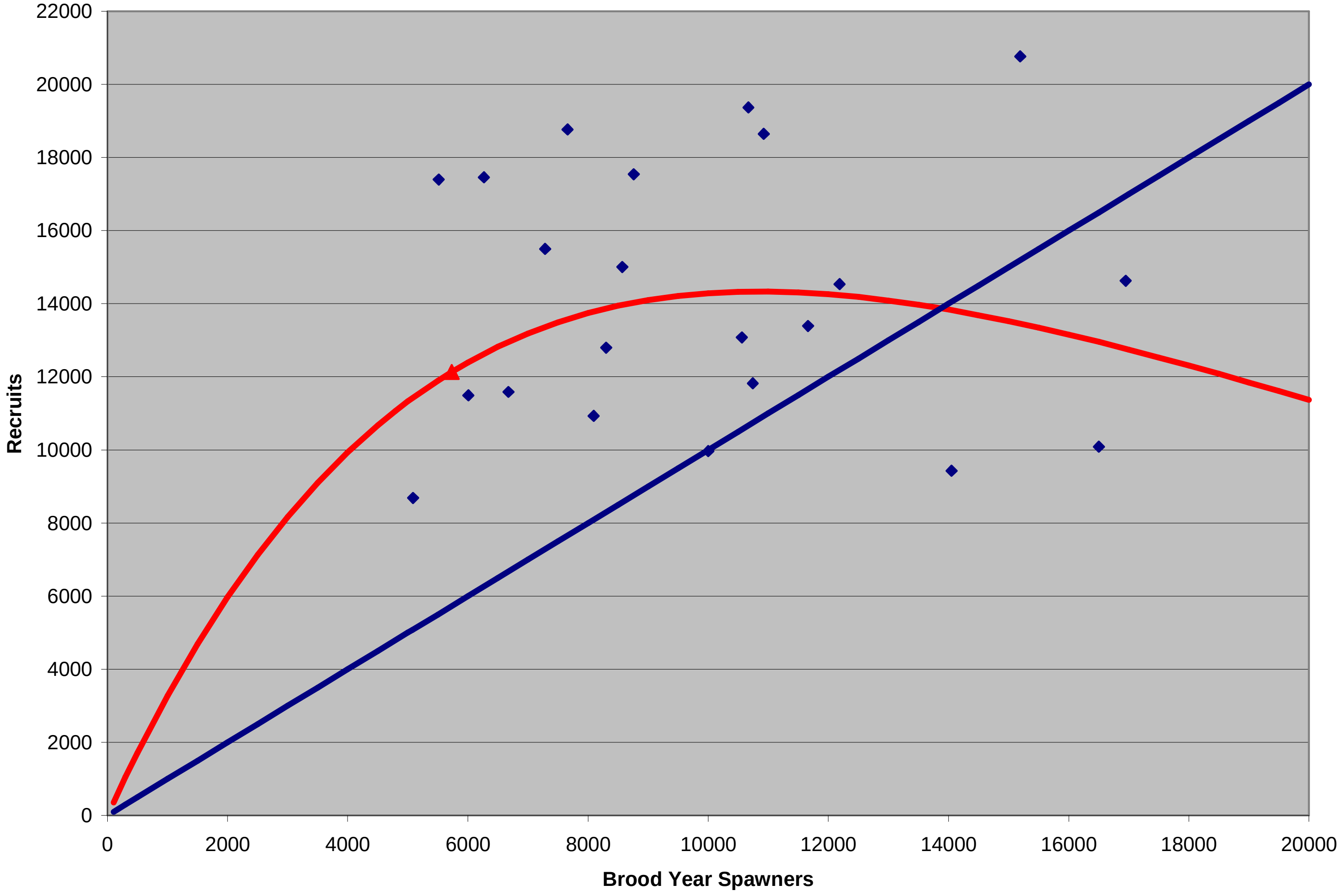

Figure 1

Figure 2.

Ricker and Beverton-Holt Stock-Recruit Curves with common alpha (3.59) and the equilibrium values (13,875). MSY escapement levels are indicated by the red triangle on the Beverton-Holt curve and the dark blue circle on the Ricker curve.

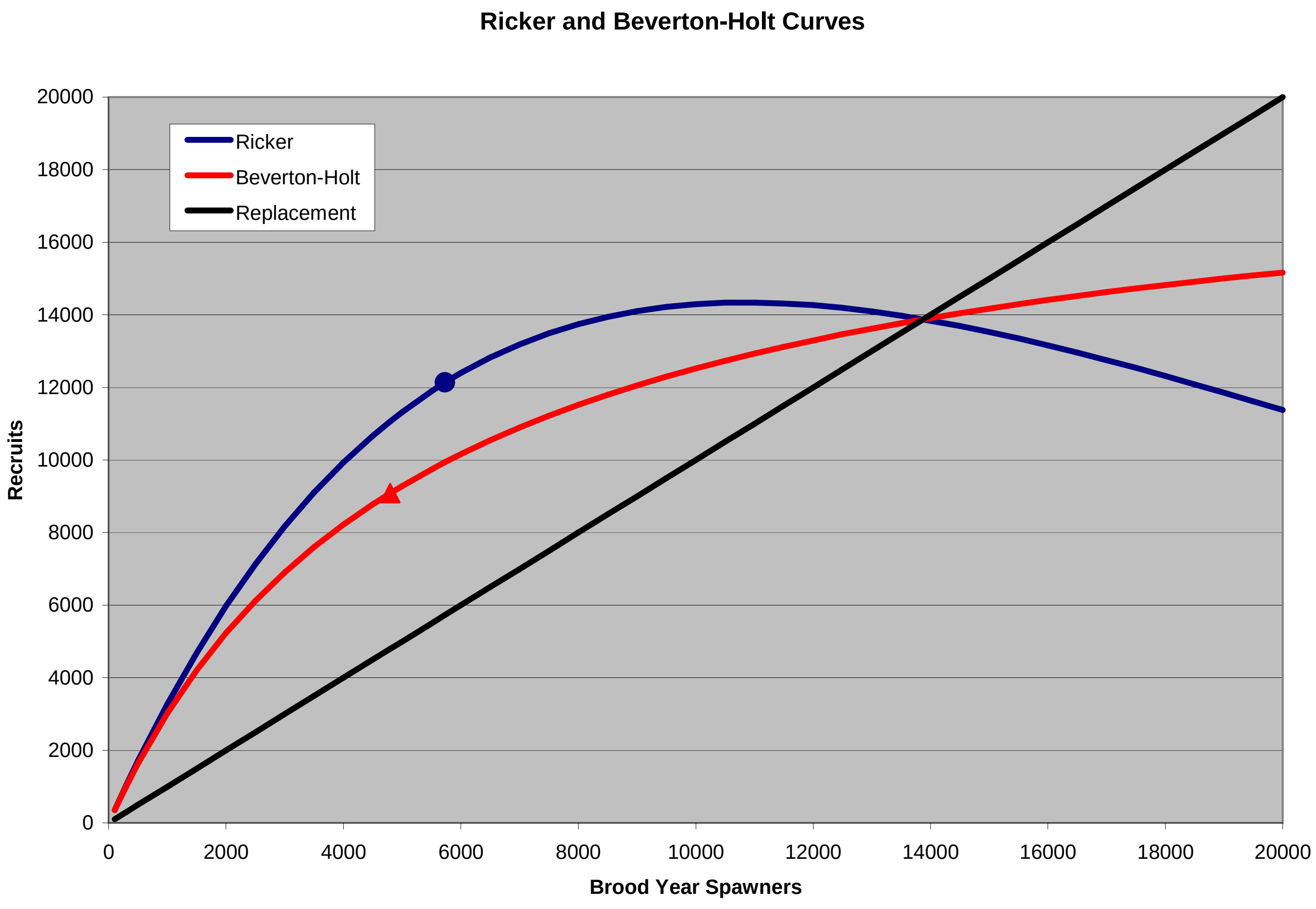

Figure 2

Figure 3.

Natural Logarithm of Residuals from Best Fit of Quilleute Winter Steelhead Data to Ricker Equation for Brood Years 1978 to 1999.

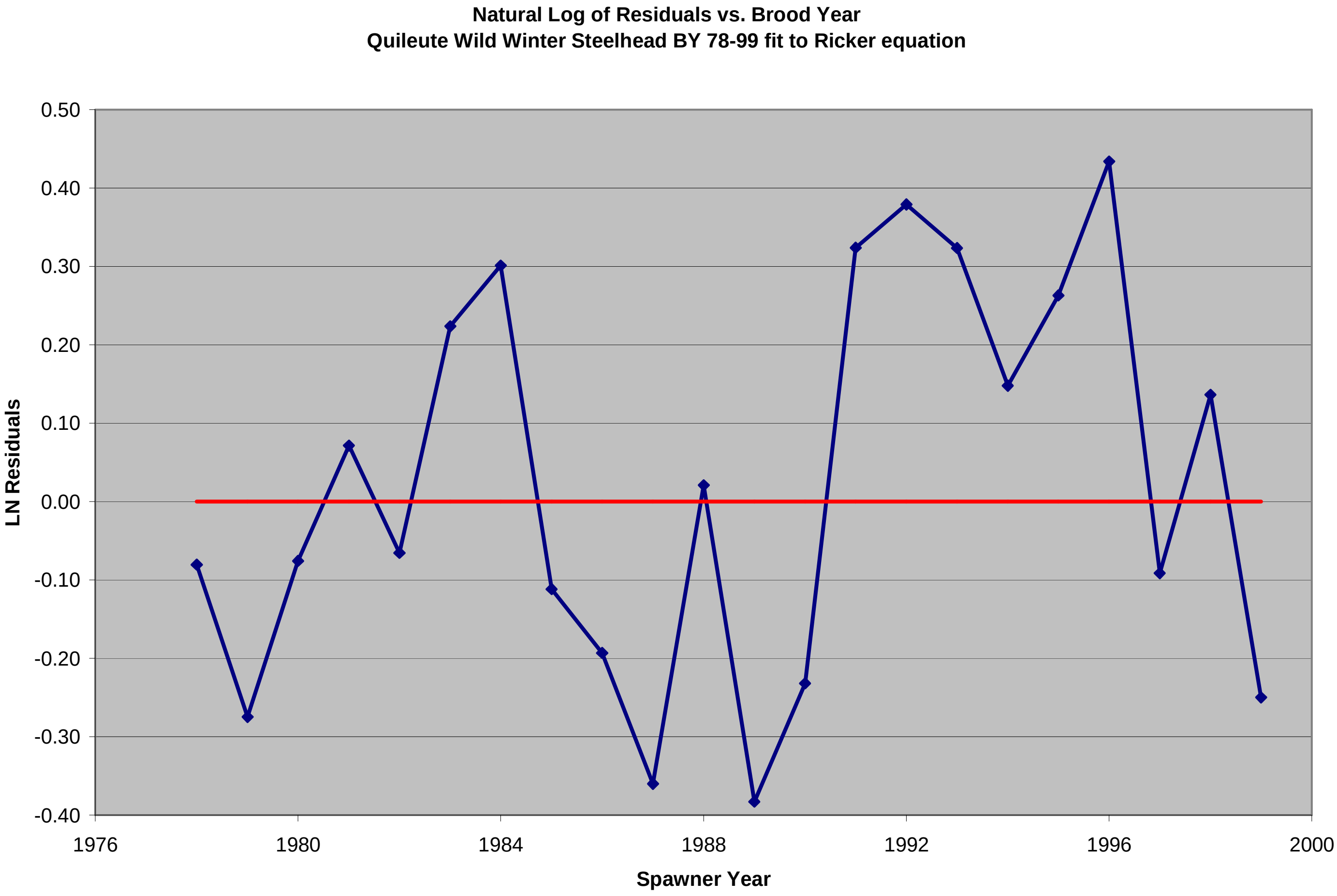

Figure 3.

Figure 4.

Skagit wild Winter-Run Steelhead for Brood Years 1978 to 1996.

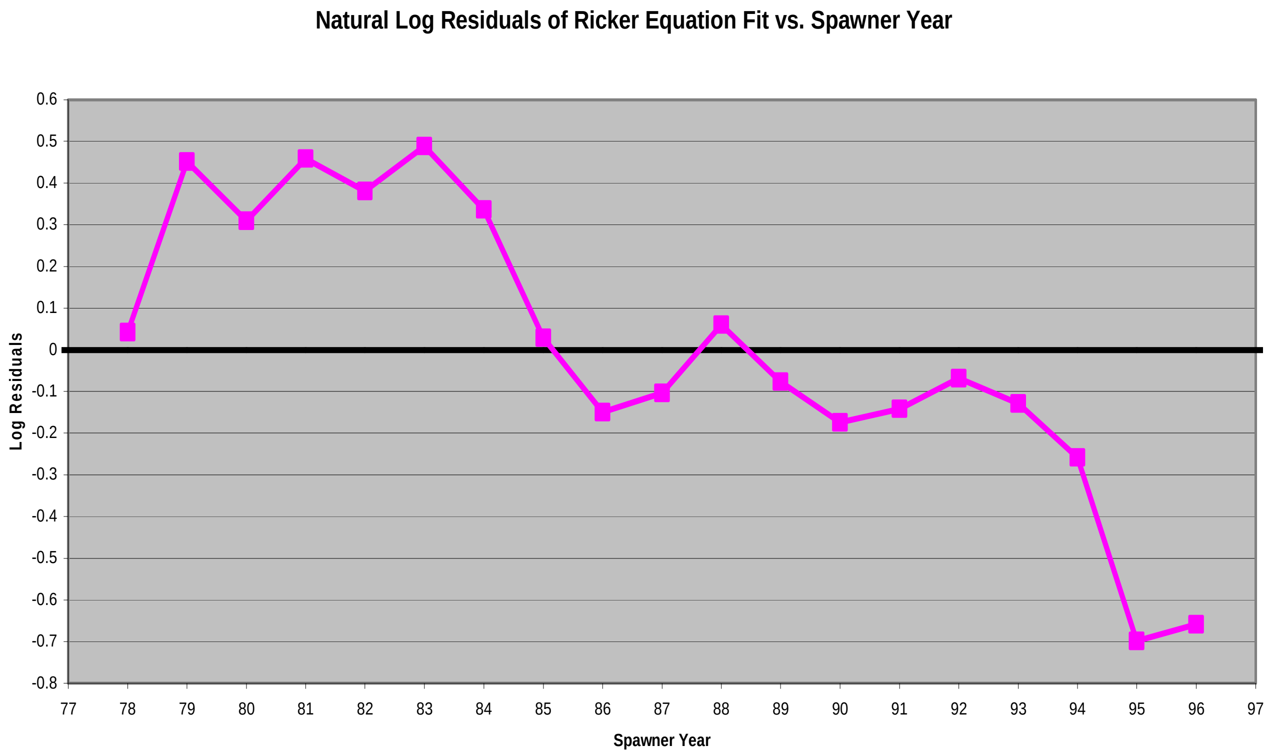

Figure 4.

Figure 5.

Posterior Distribution of Ricker alpha parameter from fit to Quilleute winter steelhead run data for brood years 1978 – 1999.

Priors on alpha: uniform (2.0, 8.0); beta: uniform (3000, 20000); residual standard deviation, sigma: uniform (0.05. 2.0).

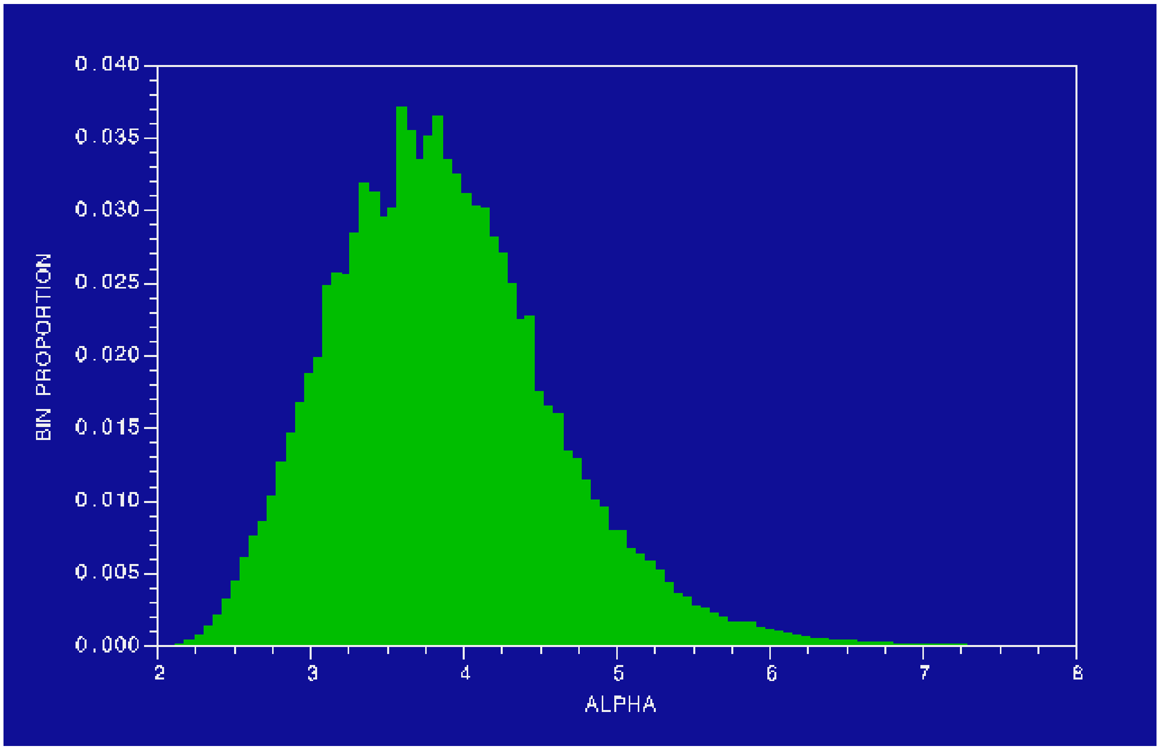

Figure 5

Figure 6.

Posterior Distribution of Ricker beta parameter from fit to Quilleute winter steelhead run data for brood years 1978 – 1999.

Priors on alpha: uniform (2.0, 8.0); beta: uniform (3000, 20000); residual standard deviation, sigma: uniform (0.05. 2.0).

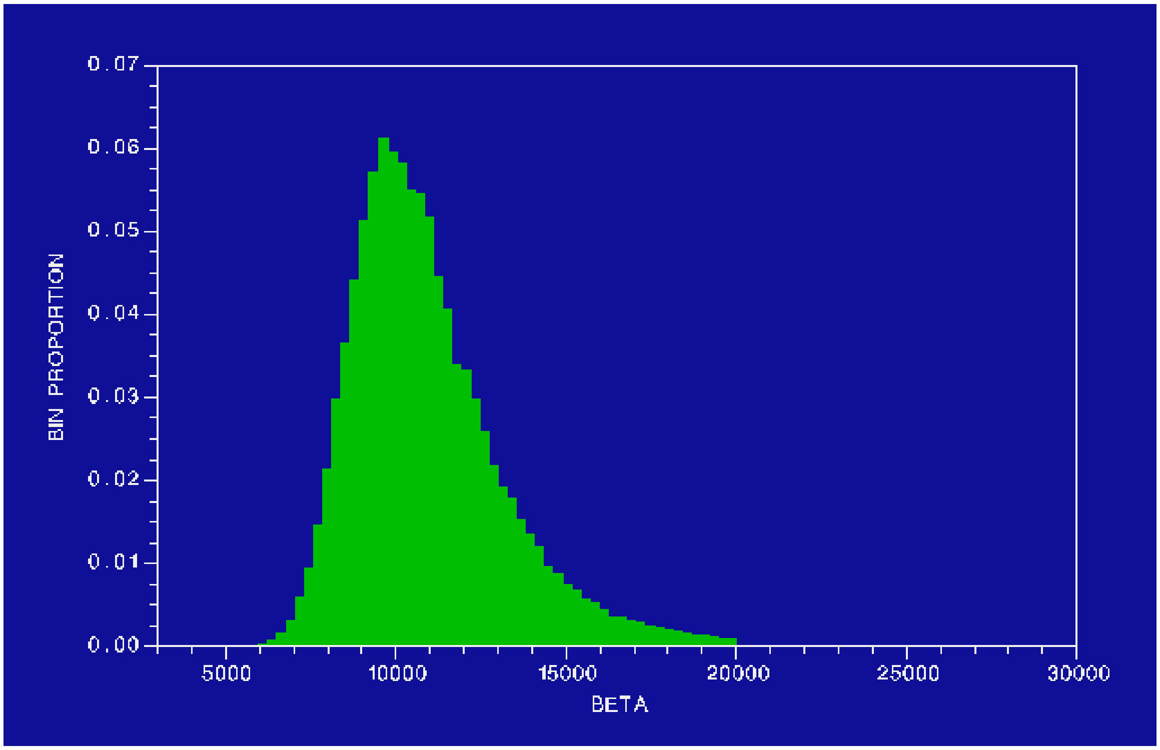

Figure 6

Figure 7.

Posterior Distribution of residual standard deviation of Ricker from fit to Quilleute winter steelhead run data for brood years 1978 – 1999. Priors on alpha: uniform (2.0, 8.0); beta: uniform (3000, 20000); residual standard deviation, sigma: uniform (0.05. 2.0).

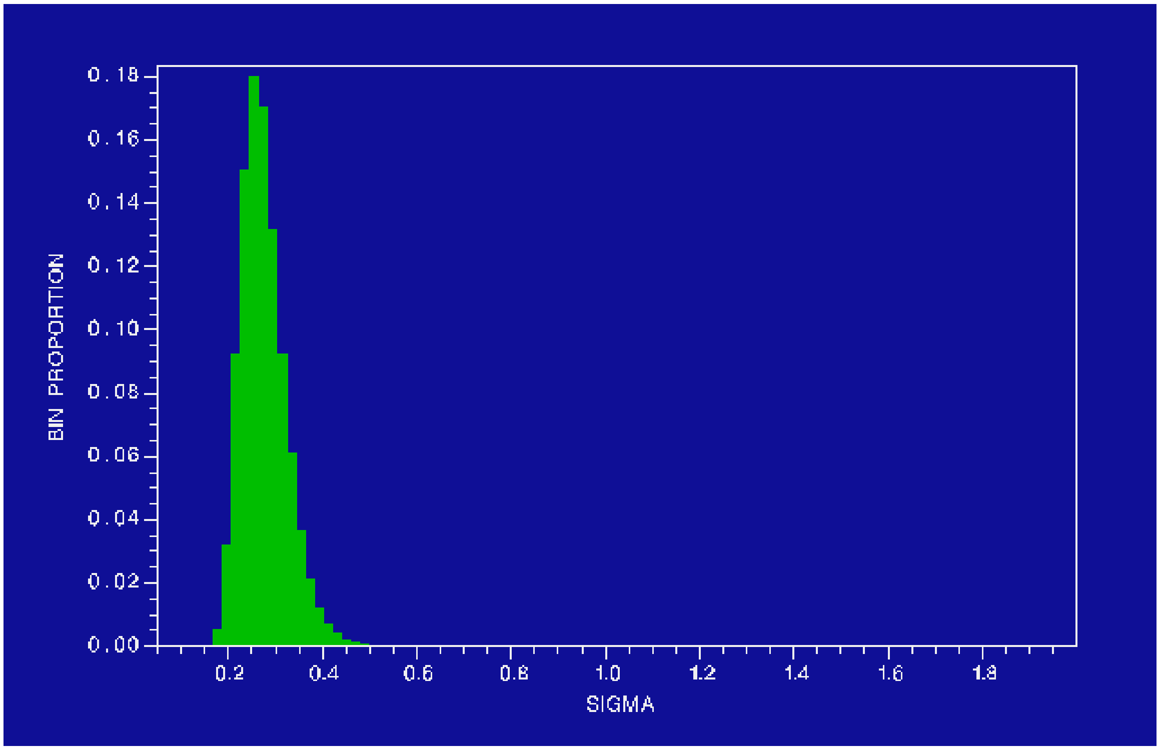

Figure 7

Figure 8.

Posterior Distribution of equilibrium abundance EQ from the joint posterior distribution of the alpha and beta parameters of the fit of the Ricker equation to Quilleute winter steelhead run data for brood years 1978 – 1999, using the relationship EQ = Ln(alpha)*beta. Priors on alpha: uniform (2.0, 8.0); beta: uniform (3000, 20000); residual standard deviation, sigma: uniform (0.05. 2.0).

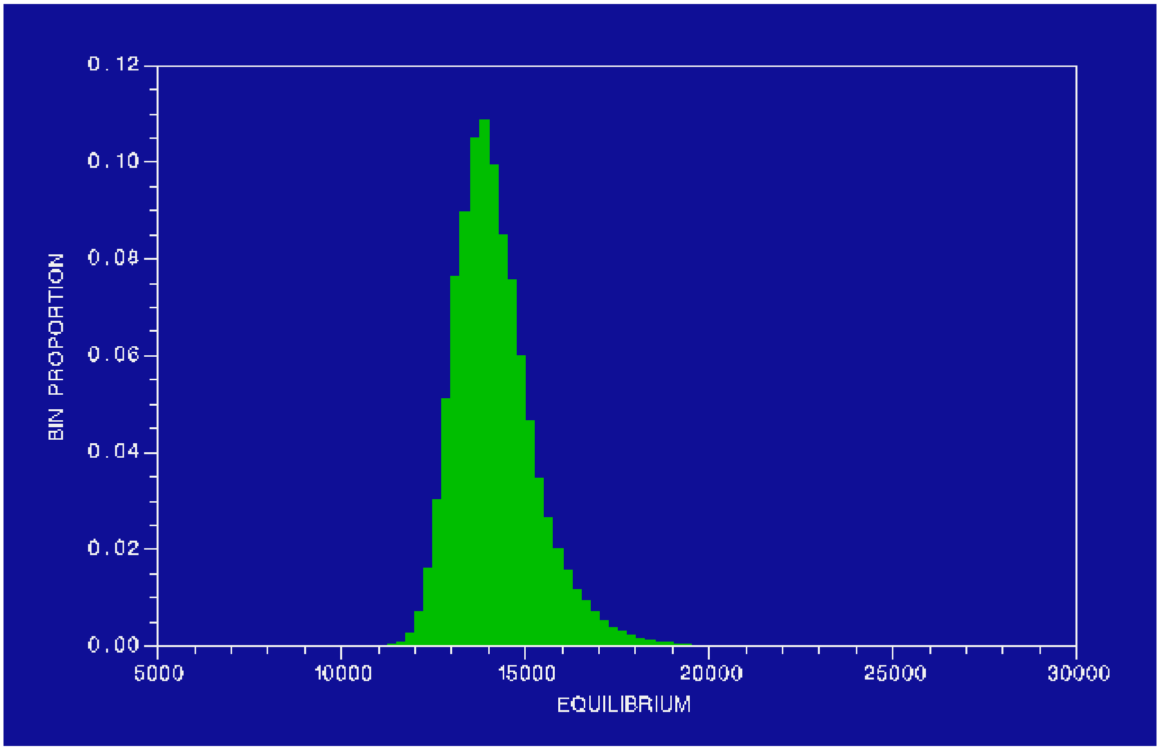

Figure 8

Figure 9.

Left Cumulative Posterior Distribution of equilibrium abundance EQ from the joint posterior distribution of the alpha and beta parameters of the fit of the Ricker equation to Quilleute winter steelhead run data for brood years 1978 – 1999, using the relationship EQ = Ln(alpha)*beta. Priors on alpha: uniform (2.0, 8.0); beta: uniform (3000, 20000); residual standard deviation, sigma: uniform (0.05. 2.0).

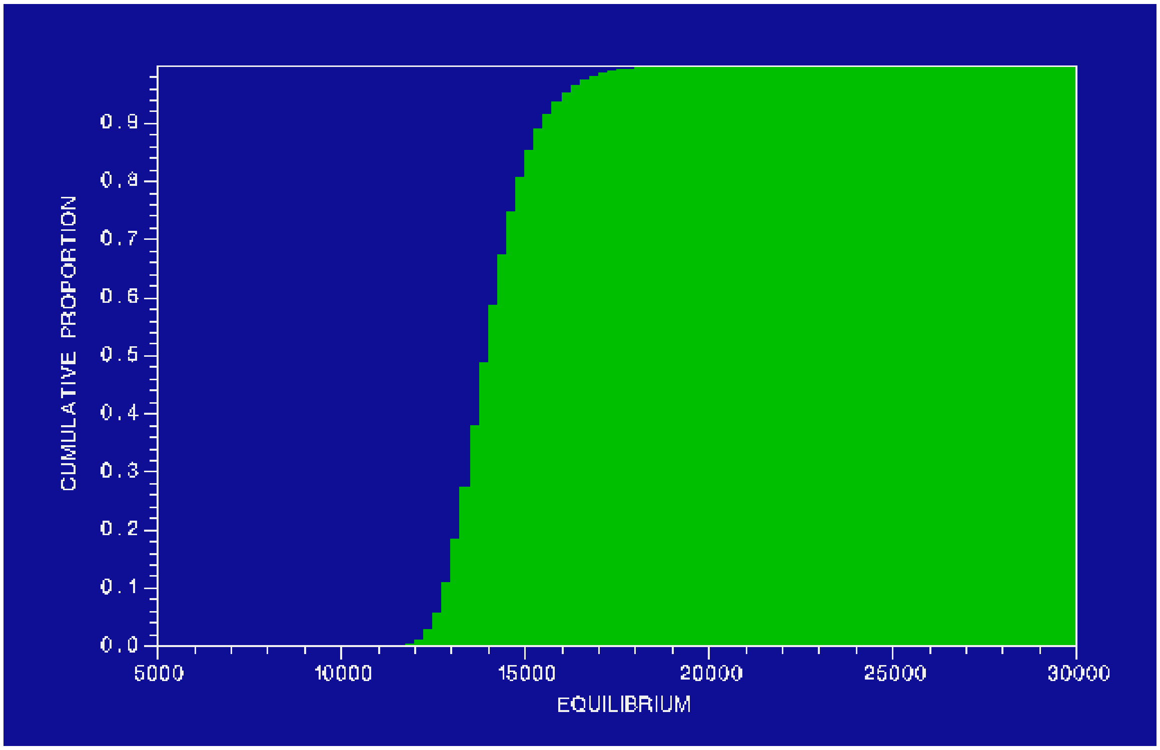

Figure 9