Alaska Hatchery Research Program | **Technical Document:**[1] 1

Title: Defining relative reproductive success: which fish count? **Version:** 1.0
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Abstract

How the Alaska Hatchery Research Group defines reproductive success will have implications on how the fitness effects of hatchery fish on natural populations are estimated. Here we present: 1) a proposed mathematical definition for relative reproductive success from the literature, 2) different definitions of "potential parent" and "adult offspring" used to estimate reproductive success and how these definitions affect the determination of relative reproductive success, and 3) concerns about the necessary changes to field sampling in 2014 to accommodate different definitions of reproductive success. We recommend that reproductive success be based in the context of management by escapement by including as many F_0 potential parents and F_1 potential offspring as possible, including those that produce no adult offspring such as pre-spawn mortalities in order to determine productivity in relation to escapement.

Background of AHRG

Extensive ocean-ranching salmon aquaculture is practiced in Alaska by private non-profit corporations (PNP) to enhance common property fisheries. Most of the approximately 1.7B juvenile salmon PNP hatcheries release annually are pink salmon in Prince William Sound (PWS) and chum salmon in Southeast Alaska (SEAK; Vercessi 2013). The large scale of these hatchery programs has raised concerns among some that hatchery fish may have a detrimental impact on the productivity and sustainability of natural stocks. Others maintain that the potential for positive effects exists. ADF&G convened a Science Panel (Alaska Hatchery Research Group; AHRG) whose members have broad experience in salmon enhancement, management, and natural and hatchery fish interactions. The AHRG was tasked with answering three priority questions:

I. *What is the genetic stock structure of pink and chum salmon in each region (PWS and SEAK)*?

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II. *What is the extent and annual variability in straying of hatchery pink salmon in PWS and chum salmon in PWS and SEAK*?

III. *What is the impact on fitness (productivity) of natural pink and chum salmon stocks due to straying of hatchery pink and chum salmon*?

Introduction

Measuring the Impact on Fitness

To answer the third question, we need to know the origin and pedigree of each fish captured in select streams across multiple generations. **Origin** refers to the type of early life-history habitat (hatchery or natural) that a fish experienced. **Pedigree** refers to the family relationship among parents and offspring. **'Ancestral origin'** refers to the origin of an individual's ancestors (e.g., two parents of a single origin [hatchery/hatchery or natural/natural] or two parents of mixed origin [hatchery/natural]). These ancestral origins can be determined by combining information from three sources: natural or hatchery origin from otolith marks, pedigree from genetic data, and age from scales (for chum salmon from SEAK). By pairing these data within fish and across generations, we can estimate **reproductive success** (**RS**) among cross types (i.e. hatchery-hatchery, hatchery-natural, and natural-natural origin crosses). The AHRG is using the **relative reproductive success** *(***RRS***) of hatchery-origin fish to natural-origin fish as the measure of fitness in this study*.

Problem: What is Relative Reproductive Success?

The RRS of hatchery-origin to natural-origin fish can be calculated in multiple ways depending upon the definition of RS. *The* **average RS**, *or* **fitness**, *of a group is defined in the AHRG priority questions as productivity*. **Productivity** of a system is typically defined as the average number of adult offspring (F_1 recruits) per potential parent (F_0 spawners). The exact definition of both **'potential parent'** and **'adult offspring'** is not clear in this study and can be defined as *one of five categories of adults observed in or near freshwater streams* (Figure 1). Different definitions of 'potential parent' and 'adult offspring' produce different measures of RS and require different field sampling procedures in order to accurately estimate F_0 potential parents and F_1 adult offspring. The AHRG needs to decide upon a definition of potential parent and adult offspring prior to the 2014 summer field season to guarantee that the data collected will be able to adequately answer the proposed research questions.

Goals of Technical Document

Four goals of this technical document are to:

1) Propose a mathematical definition of RRS from the literature (Araki and Blouin 2005);
2) Explain how the definition of potential parent and adult offspring affects RS and the estimation of RRS;
3) Describe how different definitions of RS require different field sampling methods; and
4) Request a decision by the AHRG on the definition of RS prior to the 2014 field season.

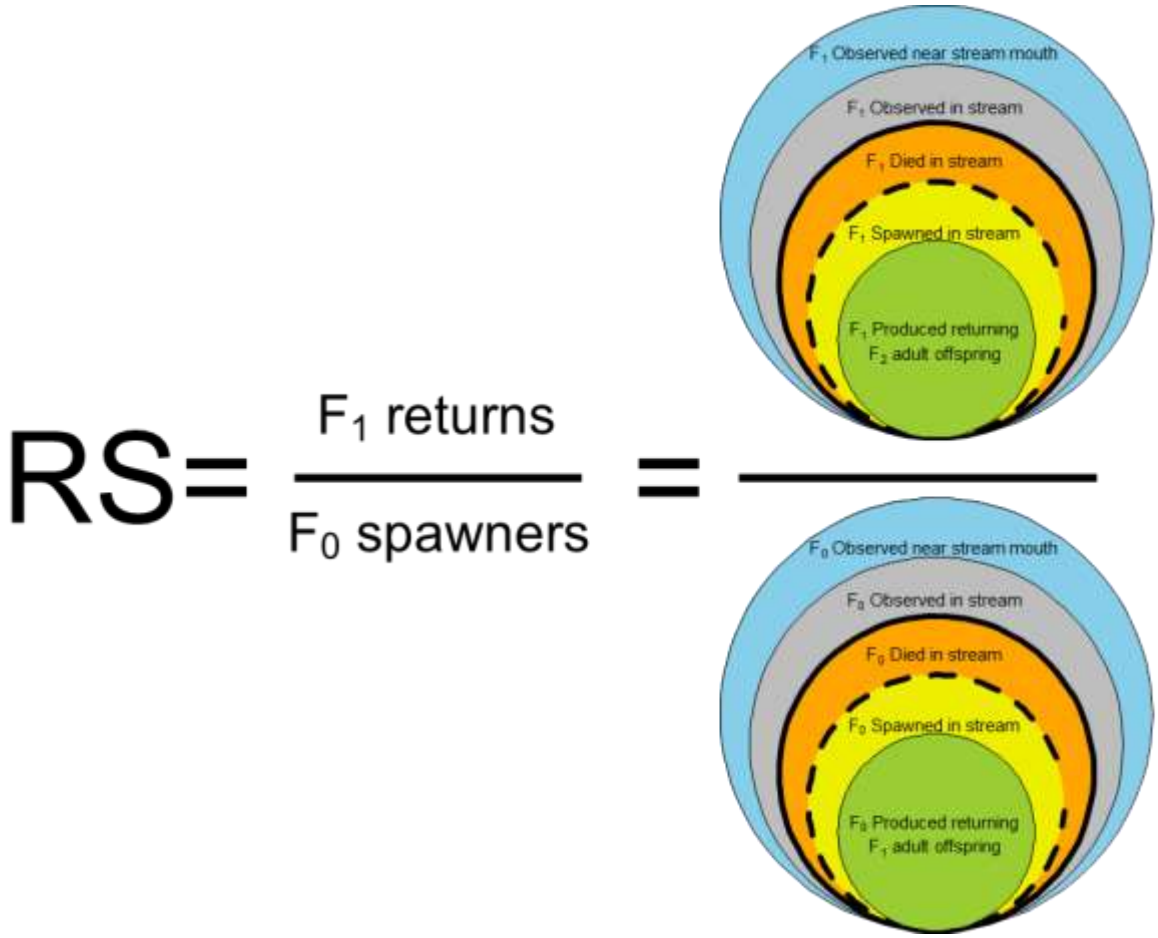

Figure 1: Equation for RS depends on which category of "adult offspring" and "potential parent" observed in streams is included in the numerator and denominator, respectively. Five definitions of adults and offspring can be visualized as concentric circles. The orange (bold) and yellow (dashed) shaded circles are different definitions of "potential parent" and "adult offspring" that require different field sampling methods regarding the inclusion of pre-spawn mortalities. The largest, most inclusive circle is what managers' observe during aerial surveys of escapement.

Mathematical Definition of RRS

While the intuitive definition of RS (i.e. number of F_1 returns per number of F_0 spawners) works well in situations where there is little to no error in parentage assignment and all parents are sampled, research has shown that both parentage assignment error and failure to sample all parents can lead to biases in RS and RRS. Given that some level of parentage assignment error is unavoidable and that in this study not all parents will be sampled, it is important to use and unbiased estimate of RS and RRS. Below are the formulas and definitions used to calculate an unbiased estimate of RRS ($RRS_{[\text{unbiased}]}$) as published by Araki & Blouin (2005). Observed mean fitness ($\widehat{W}_x$) of a group 'x' is a commonly used measure of RS for that group. However, there are five potential definitions of RS for individuals in a given group. We will expand on these five definitions and their implications in the following section.

$$RS_{x[unbiased]} = W_x = \left(\frac{1}{1-\hat{a}}\right)\left[\widehat{W}_x - \left(\frac{N_{offspring} - N_{assigned}}{N_{parent}}\right)\left(\frac{\hat{b}}{1-\hat{b}}\right)\right] \quad \text{(Eq. 13; Araki \& Blouin 2005)}$$

$$RRS_{x/y[unbiased]} = \frac{\widehat{W}_x - \left(\frac{N_{offspring} - N_{assigned}}{N_{parent}}\right)\left(\frac{\hat{b}}{1-\hat{b}}\right)}{\widehat{W}_y - \left(\frac{N_{offspring} - N_{assigned}}{N_{parent}}\right)\left(\frac{\hat{b}}{1-\hat{b}}\right)}$$ (Eq. 14; Araki & Blouin 2005)

where

$\widehat{W}_x$ = observed mean (absolute) fitness of individuals in group x;

$\widehat{W}_y$= observed mean (absolute) fitness of individuals in group y;

$N_{offspring}$ = number of offspring sampled;

$N_{assigned}$ = number of offspring assigned to a parent;

N_{parent} = number of potential parents sampled from groups x and y;

a = rate of *failed* parentage assignments (*exclusion*) when *true* parent is sampled; and

b = rate of incorrect assignments (i.e. *assignment* to an *untrue* parent).

The assignment error rates a and b are calculated as

$$\hat{a} = 1 - \frac{(1-\alpha)P_{assigned}}{P_{offspring}}$$ (Eq. 30; Araki & Blouin 2005)

$$\hat{b} = \frac{\alpha P_{assigned}}{1-(1-\alpha)P_{assigned}}$$ (Eq. 31; Araki & Blouin 2005)

where

α = threshold probability of incorrect assignments (i.e. *assignment* to an *untrue* parent) used in likelihood-based or Bayesian-based parentage assignment to accept/reject a parent-offspring pairing

x = number of potential parents from group x

y = number of potential parents from group y

$$P_{assigned} = \frac{N_{assigned}}{N_{offspring}}$$ (Appendix I; Araki & Blouin 2005)

$$P_{offspring} = \frac{xW_x + yW_y}{N_{offspring}}$$ (Eq. 23; Araki & Blouin 2005)

When both $a = 0$ and $b = 0$, then $RS_{\text{[unbiased]}} = \widehat{W}_x$ and $RSS_{\text{[unbiased]}} = \frac{RS_x}{RS_y} = \frac{\widehat{W}_x}{\widehat{W}_y}$. In addition, while a is usually not known (i.e. it is dependent on $P_{offspring}$ which is usually not known), estimation of $RRS_{\text{[unbiased]}}$ only requires b (which is independent of $P_{offspring}$).

Defining RS

Potential Definitions of RS

The previously described mathematical methods of estimating of $RRS_{[\text{unbiased}]}$ are dependent upon the definition of both "potential parents" in the denominator and "adult offspring" in the numerator of RS (Figure 1), where RS is analogous to the observed population mean fitness ($\widehat{W}_x$ and $\widehat{W}_y$) in the equations from Araki & Blouin (2005). We use a hypothetical example to illustrate how the definition of "potential parents" in RS affects RRS by comparing recruits-per-spawner data from two hypothetical groups (Group X and Group Y) under different definitions of "potential parents" (Figure 2). Figure 2 shows distributions of the proportion of parents that have a given number of offspring assigned to them after incorporating variation in family size (note the colors are the same as in Figure 1 with the exception that F_0's near the stream mouth [blue] are not shown). Variation in family sizes of salmon populations can be quite large and should be considered when assessing genetic variation and short-term population dynamics, especially given that many families produce zero returning adults (Geiger et al. 2007). To realistically incorporate variance in family size, we randomly sampled from a negative binomial distribution based upon the simulation work of Anderson et al. (2011).

When "potential parents" are defined as all F_0's observed in the stream (Figure 1 & 2), the proportion of parents that produced zero offspring is represented by the gray bar (including all colors, except blue in Figure 1). Using this measure of F_0, the RRS of Group X to Group Y is calculated as:

$$RS_x = 3.0 \text{ and } RS_y = 1.0\text{, giving an estimated } RRS = 3.0.$$

However, when "potential parents" are defined as only F_0's that produced returning F_1 adult offspring as has been proposed for the AHRG, the proportion of parents that produced zero offspring is not represented (only green bars). Using this measure of F_0, the RRS of Group X to Group Y is calculated as:

$$RS_x = 4.3 \text{ and } RS_y = 1.9\text{, giving an estimated } RRS = 2.3.$$

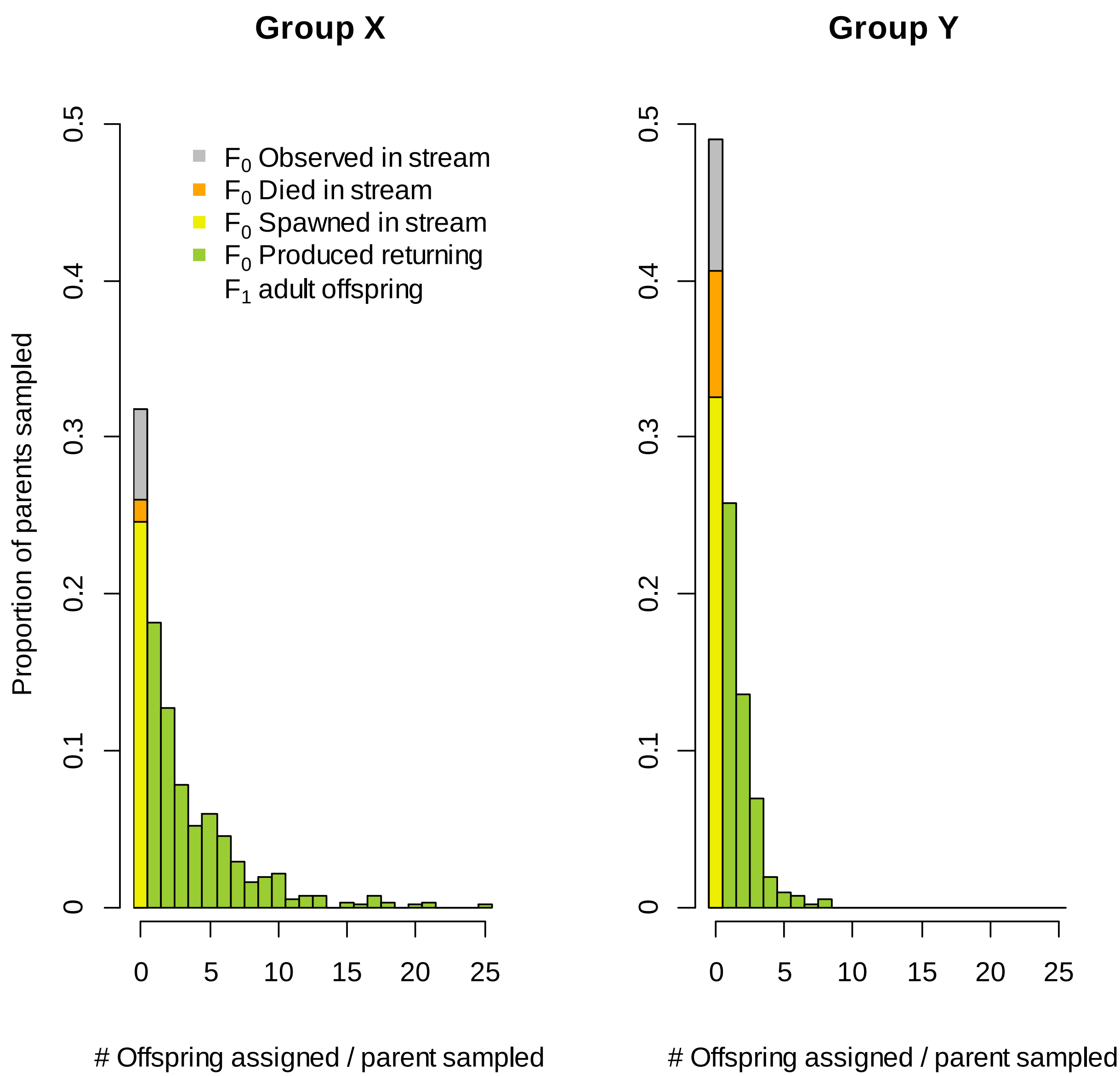

Figure 2: Hypothetical data from two groups, X and Y. Note the large difference in the proportion of parents that produced zero offspring under different definitions of "potential parents" and the implications this has for calculating RS and estimating RRS.

Example from Literature

Recently Hess et al. (2012) investigated the fitness impacts of a supportive breeding hatchery program on a natural population of Chinook salmon in the South Fork Salmon River of the Columbia River Basin. This study estimated RSS using the equations from Araki & Blouin (2005) based on two definitions of RS (method [i] and [ii]) that differed in how they defined "potential parents" (denominator of RS; Figure 1). Method (i), which they reported in supplemental information, includes all F_0 parents observed in the stream (e.g., gray in Figure 1 & 2) regardless of whether they produced any adult progeny in the denominator thus allowing RS to vary from $0 \rightarrow \infty$,

$$RS = \frac{\#\ F_1\ Returns}{\#\ F_0\ Observed\ in\ stream} \qquad \text{Method (i)}$$

Method (ii), which was used in the body of the paper, includes only parents that are known to have produced adult progeny (i.e. parents that have at least 1 offspring assigned; green in Figure 1 & 2) in the denominator thus restricting RS to vary from $1 \rightarrow \infty$,

$$RS = \frac{\#\ F_1\ Returns}{\#\ F_0\ Produced\ returning\ F_1\ adult\ offspring} \qquad \text{Method (ii)}$$

When Method (ii) was used to calculate RS over two brood years (1998 & 2000) the average RRS$_{♀}$ = 1.11 and RRS$_{♂}$ = 0.89 (Table 2 in Hess et al. 2012). However, Method (ii) does *not* capture differences in the proportion of parents that produce no adult offspring among ancestral groups (hatchery vs. natural). Method (i) of calculating RS *does* incorporate the difference in proportion of parents that produce no adult offspring among ancestral origins and resulted in the average RRS$_{♀}$ = 1.00 and RRS$_{♂}$ = 0.64 for same period (Table S3 in Hess et al. 2012). This is an important consideration given that differences in the mating success among ancestral origins have been documented in other salmonids (Chinook, Anderson et al. 2013; coho, Thériault et al. 2011). It is also important to note that since the authors had data from every fish that passed a weir, they were able to present their results in different ways, rather than being forced into a definition of RS by limitations to the data.

Incorporating Relative Reproductive Success into Spawner-Recruit Curves

Differences in RRS among ancestral origins will influence spawner-recruit curves (and therefore setting of escapement goals) depending on whether ancestral origin affects reproductive success and when density-dependent forces occur. For example, if density-dependent forces take place during spawning (i.e. redd super-imposition) and ancestral origin does not affect redd digging location, then the number of fish entering the stream is the best measure of that force. On the other hand, if density-dependent forces occur after hatch (i.e. oxygen levels in the gravel) and fish of different ancestral origins have different hatch rates, then the best measure of force might be the number of successfully spawning fish. This is a complex issue that will need to be addressed by the AHRG in a future technical document.

Spawner-recruit relationships are traditionally calculated based on escapement data, because no information is available on the number of fish successfully contributing to the next generation. Escapement for pink salmon in PWS is often estimated from aerial stream surveys in which managers count all fish in-river (alive and dead) and/or milling in the inter-tidal zone at the mouth of stream. Inclusion of either all live fish in stream or at least all fish that died in a stream (gray and orange in Figure 1 & 2) is likely more relevant to managers as it most closely puts RS into the context of escapement by including the largest number of potential parents as counted in stream surveys.

Implications of Definitions of "Parents" and "Offspring" on Field Sampling

If the inclusion of all fish observed in the stream (gray in Figure 1 & 2) is chosen as the measure of F_0 for estimating RS (as opposed to other more restrictive measures), this would result in a tradeoff between sampling a higher proportion of adults that do not contribute to the next generation (i.e. fish that are 'nosing in') and increasing the probability of sampling all contributing adults.

If the inclusion of all fish that died in a stream (orange in Figure 1 & 2) is chosen as the measure of F_0 for estimating RS, then it is important to include pre-spawn mortalities in the field sampling, because it will affect the number of potential parents (denominator of RS; Figure 1). We recommend that pre-spawn mortalities be sampled for otoliths (to determine ancestral origin) but not genetic tissues for the initial years of the study where only F_0 is being measured (2013-2014; Figure 3).

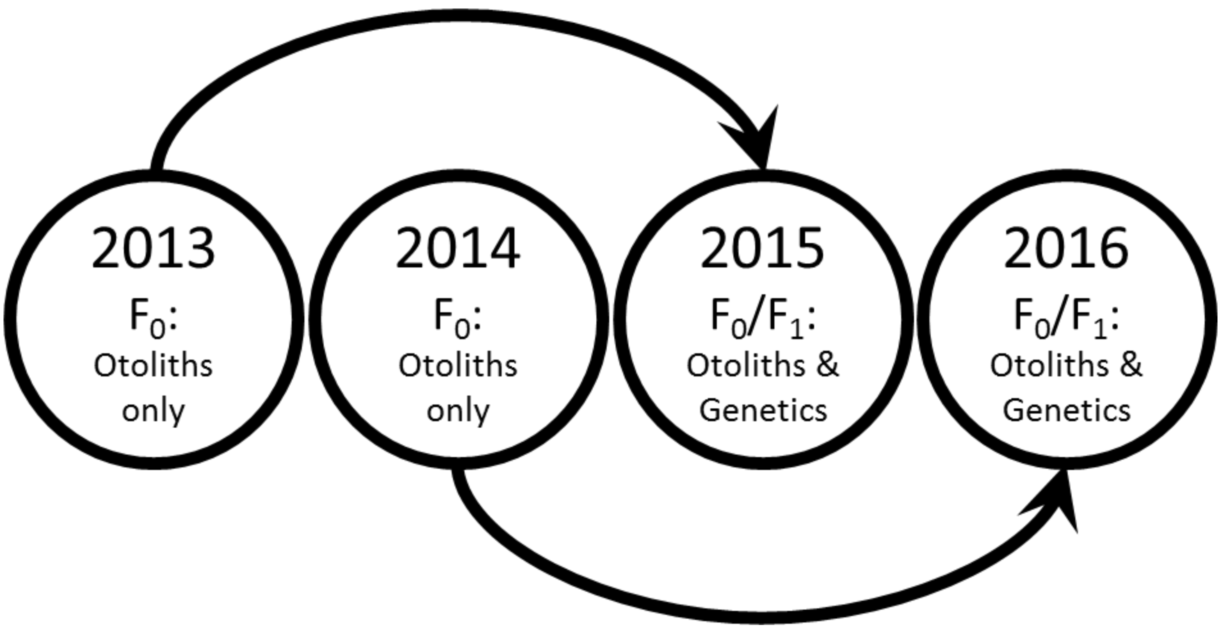

Figure 3: Example sampling strategy for pre-spawn mortalities for pink salmon in PWS.

If potential parents are defined as all fish that died in the stream, then knowledge of the ancestral origin of pre-spawn mortalities is important because they are included as potential parents in the calculation of RS (Figure 1 & 2). However, to maximize our ability to use genetic data to infer pedigrees it is not necessary to take a genetic sample from pre-spawn F_0 fish, as they are not likely to produce any F_1 adult offspring. Yet for years of this study in which F_1's are being sampled (2015-2016), it is important to obtain both otoliths and a genetic sample from pre-spawn mortalities, as pre-spawn mortalities may include F_1 recruits (Figure 3). It is important to note, however, that sampling only dead fish will inherently result in a higher probability of missing contributing adults since it will not be possible to sample every dead fish (i.e. they may wash out, etc.).

Failure to sample pre-spawn mortalities in the field may provide inaccurate estimates of RS in the context of escapement data, because managers implicitly assumed them to be potential parents when counted in aerial stream surveys of escapement. It is important to recognize that pre-spawn mortalities can always be excluded from future analyses if we have the field data, but that they will not be able to be included if we do not have the field data. Obtaining field data on the greatest number of F_0's possible will allow for both the ability to answer a greater range of questions **and** increased statistical power to answer those questions. Due to changes in the experimental design regarding a reduction in the number of "alevin streams" being sampled, there are adequate resources to genotype additional adults.

Summary Table

	Definitions of "potential parent"			
	Present in stream	*Died in stream*	*Spawned in stream*	*Contributed F_1*
Pros	Escapement puts RS in a management context. Maximizes probability of sampling contributing fish.	Similar to escapement, incorporates differences in spawning success by origin (H vs. N)	Maximizes efficiency of field sampling for pedigree	Measures family size of spawners that contribute to future generations
Cons	Costs in sampling and genotyping non-contributing parents in the spring of 2014	Reduces probability of sampling contributing fish. Differential field sampling of pre-spawn mortalities (i.e. otoliths only in F_0 years, otoliths and genetics in F_1 years).	Reduces probability of sampling contributing fish. Does not incorporate differences in spawning success by origin (H vs. N)	Depending on sampling methods, may reduce probability of sampling contributing fish. Does not incorporate differences in spawning success by origin (H vs. N).

Other Issues Mentioned, but Not Discussed

- Differences in measuring RRS for individual parents vs. cross types (parent pairs)
- Measuring density-dependent forces
- Sampling of F_1 recruits in 2015/2016

Questions for the AHRG

1. Should we use RRS as defined by Equation 14 of Araki & Blouin (2005)?
2. How should we define both "potential parents" and "potential offspring" in the equation of RS (Figure 1)? Should our calculation of RS attempt to mirror escapement as closely as possible?
3. Should pre-spawn mortalities be included in field sampling, as recommended by the ADF&G Gene Conservation Lab?

AHRG Review and Comments

This technical document was discussed at the December 12, 2014 meeting of the AHRG. In addition it was reviewed by email exchange prior to the meeting.

The AHRG did not specifically answer questions 1 and 2, electing to address them at a later date. It is recommended to sample pre-spawn mortalities.

This document is acceptable to the AHRG.

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