

RRS2E

A statistical tool to estimate the relative reproductive success of hatchery-origin spawners with multiple years of data

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SUMMARY

A maximum likelihood estimator of relative reproductive success (RRS) and its variance were derived when multiple years of data are available.

INTRODUCTION

The presence of hatchery-born spawners is believed to influence reproductive success on the spawning grounds in many ways, yet its actual effect on recruits per spawner remains one of the greatest unknowns hampering the estimation of long-term population trends of salmonid populations. When hatchery-born fish are allowed to interbreed with wild-born fish on spawning grounds (i.e., the wild population is supplemented), the productivity of naturally spawning populations may be reduced, compromising conservation objectives (Reisenbichler and Rubin 1999). Even when hatchery spawners do not affect the reproductive success of wild-born spawners, hatchery-born spawners can still impede the estimation of trends in the wild portion of the population (Hinrichsen 2003; McClure et al. 2003). To see this, suppose that a large total recruitment per wild spawner is evident in the retrospective spawner series. If hatchery-reared spawners are as effective at producing adult progeny as wild fish, then the large total recruitment per wild spawner could have been due to a large input of hatchery-born spawners one generation ago, even though the trend in wild population abundance was downward. At the other extreme, if hatchery-born spawners produce no adult progeny (recruits), then a large total recruitment per wild-born spawner indicates a clear upward trend in wild population abundance. Reliably estimating the relative reproductive success of hatchery-born spawners (RRS) is also important for evaluating the effectiveness of captive rearing programs as a restoration strategy (Fleming 1994; Berejikian et al. 1997).

Because of its importance and advances in genetic tagging, studies of the relative reproductive success of hatchery-born spawners have increased over the last two decades. In early studies, Chilcote et al. (1986) used electrophoretic methodologies of Allendorf (1975) to estimate differential reproductive success of hatchery and wild summer-run steelhead (*Oncorhynchus mykiss*) under natural conditions. They concluded that the success of hatchery

fish in producing smolt offspring was only 28% that of wild fish. This work was later expanded by Leider et al. (1990), who showed that relative reproductive success of naturally spawning hatchery steelhead compared with wild steelhead decreased from 0.75–0.788 at the subyearling stage to 0.108–0.129 at the adult stage. Later investigations by Garant et al. (2001) and Taggart et al. (2001), used a pedigree analysis whereby parents (spawners) were assigned to offspring (adult returns) using DNA analysis. This approach uses genetic differences among individuals to assess fitness. It differs from the approach of earlier experiments of Reisenbichler and McIntyre (1977), Leider et al. (1990), and Fleming et al. (2000) that used genetic markers that differentiated among groups of spawners, not individuals. The advantage of the group-based approach is that it requires few genetic markers; its disadvantage is that it requires good genetic differentiation between groups and, unlike the individual approach, does not provide individual fitness data, which can be used to estimate fitness with respect to individual traits such as run timing, size, or age (Morgan and Conner 2001). In individual-based experiments, the parents of the adult progeny (recruits) can be uniquely determined with high probability by using microsatellites, which serve as nonlethal, permanent, heritable markers (Ferguson and Danzmann 1998; Bernatchez and Duchesne 2000; Letcher and King 2001). Such experiments are expensive and exacting, requiring a high number of microsatellite loci and alleles per locus for reliable parentage assignment, but they may provide a relatively swift, accurate procedure for estimating the relative reproductive success of hatchery spawners. Recently, Hess et al. (2012), using a pedigree analysis found that mean RRS of hatchery-born females was 1.1 and that of hatchery-born males was 0.89.

The estimation of RRS is possible using the modern technique of genetic tagging called parentage-based tagging (PBT) of hatchery releases, which can be used to mark a high percentage of juveniles released. PBT involves genotyping hatchery broodstock (parents) and adding these genotypes to a database (Steele et al. 2011; Anderson and Garza 2005; Anderson and Garza 2006). Genotyped progeny of these parents collected as juveniles or adults can be assigned back to their parents, thus creating a tag identifying the origin of the parents (wild or hatchery). Software used to assign genotyped progeny to their parents, SNPPIT 1.0 developed by Anderson (2010), is available online at <http://www.mybiosoftware.com/population-genetics/6013>.

The objective of this documentation is to show how to estimate relative reproductive success of hatchery-born spawners, RRS, where hatchery-born fish are allowed to spawn naturally with wild-born fish. I developed a likelihood-based, iterative procedure for estimating the relative reproductive success of hatchery-born spawners.

METHODS

There are two basic steps for collecting spawner data necessary to estimate the relative reproductive success of hatchery-origin spawners. First, genotype adults in a certain spawning area and note their origin: hatchery or wild. Enter the genotype and origin into a parent database. Second, take a random sample from the progeny of these genotyped adults and determine which

female was its parent using parentage assignment. The progeny sampled may be juveniles or returning adults. Note the origin of the parent.

The method I develop in this documentation is a maximum likelihood technique (Mood et al. 1974). The variance of the MLE may be derived as the inverse of the Fisher Information Matrix, which is the negative of the expected value of the second derivative of the likelihood function (Mood et al. 1974). I begin by defining the assumptions (Table 1) and the variables used in the study, which are used to develop the probability model. For convenience, variable names and their definitions are given in Appendix A. Statistical code for the analysis, written in the R programming language, may be found in Appendix B.

Table 1.—Assumptions

| | |
|---|--|
| 1 | The assignment of a particular fish to a parent does not influence the assignment of any other fish to a parent (independence). |
| 2 | Each sampled fish that is the offspring of a hatchery-origin female parent has the same probability of being assigned a hatchery-origin female parent (identically distributed). |
| 3 | Each sampled fish that is the offspring of a wild-origin female parent has the same probability of being assigned a wild-origin female parent (identically distributed). |
| 4 | Whether an individual is sampled has no effect on the probability that another individual is sampled (independently drawn random sample). |
| 5 | Relative reproductive success is constant across the years of study. |

Estimation

The assumptions in Table 1 allow one to express the total number of progeny assigned to a wild-born female parent, x , as a binomial random variable with probability density function:

$$f(x) = \prod_{t=1}^T \binom{n_t}{x_t} \left(\frac{S_{W,t}}{S_{W,t} + S_{H,t}\theta} \right)^{x_t} \left(\frac{S_{H,t}\theta}{S_{W,t} + S_{H,t}\theta} \right)^{n_t - x_t} = \prod_{t=1}^T \binom{n_t}{x_t} \frac{S_{W,t}^{x_t} S_{H,t}^{n_t - x_t} \theta^{n_t - x_t}}{(S_{W,t} + S_{H,t}\theta)^{n_t}}, \quad (1)$$

where n_t is the number of progeny sampled with parents spawned in year t , T is the total number of years of spawning, x_t is the number of progeny assigned to a wild-origin female parent from brood year t , $S_{W,t}$ is the total number of wild-born female parents in brood-year t , $S_{H,t}$ is the total number of hatchery-born female parents in brood year t , and θ is the RRS of hatchery- versus wild-origin spawners. Given the joint distribution of the observations in equation (1), it is now possible to form the log-likelihood function of the unknown parameter θ by taking the natural log of the probability distribution and treating the result as a function of the parameter:

$$l(\theta) = \sum_{t=1}^T \left[\log \binom{n_t}{x_t} + x_t \log(S_{W,t}) + (n_t - x_t) \log(S_{H,t} \theta) - n_t \log(S_{W,t} + S_{H,t} \theta) \right]. \quad (2)$$

To determine the MLEs of θ , a numerical optimization routine, Fisher's Scoring Method (Jennrich and Sampson 1976), is used to maximize the log likelihood function given in equation (2). The maximization routine makes use of the derivative of the log likelihood function which is given by

$$\frac{dl}{d\theta} = \sum_{t=1}^T \left[\frac{(n_t - x_t)}{\theta} - \frac{n_t S_{H,t}}{(S_{W,t} + S_{H,t} \theta)} \right]. \quad (3)$$

In the special case where there is a single brood year of data, the MLE may be found directly by setting the right hand side of equation (3) to zero

$$\hat{\theta} = \frac{(n_1 - x_1) S_{W,1}}{x_1 S_{H,1}}, \quad (4)$$

which is the number of progeny per hatchery spawner divided by the number of progeny per wild spawner.

The next step in deriving the theoretical formulas for precision of the MLEs is to derive the Fisher Information Matrix (which is a scalar in this case, not a full matrix). The inverse of the Fisher Information Matrix will supply the variance of the MLE of θ . The Fisher Information Matrix is the negative of the expected value of the second derivative of the likelihood function. The second derivative of the likelihood function is

$$\frac{d^2 l}{d\theta^2} = \sum_{t=1}^T \left[-\frac{(n_t - x_t)}{\theta^2} + \frac{n_t S_{H,t}^2}{(S_{W,t} + S_{H,t} \theta)^2} \right]. \quad (5)$$

The Fisher Information Matrix, is given by

$$\mathbf{I} = -E\left(\frac{d^2 l}{d\theta^2}\right) = \sum_{t=1}^T \left[\frac{n_t S_{H,t} S_{W,t}}{\theta(S_{W,t} + S_{H,t} \theta)^2} \right], \quad (6)$$

and therefore the variance of the MLE is given by

$$\text{var}(\hat{\theta}) = \left\{ \sum_{t=1}^T \left[\frac{n_t S_{H,t} S_{W,t}}{\theta(S_{W,t} + S_{H,t} \theta)^2} \right] \right\}^{-1}. \quad (7)$$

The standard error of $\hat{\theta}$ is then

$$SE(\hat{\theta}) = \sqrt{\text{var}(\hat{\theta})}, \quad (8)$$

and the coefficient of variation of $\hat{\theta}$ is

$$CV(\hat{\theta}) = \frac{SE(\hat{\theta})}{\hat{\theta}}. \quad (9)$$

The MLE of RRS is calculated using Fisher's Scoring Method, which is similar to Newton's method for solving nonlinear equations (Press et al. 1992), but modified to use the

expected Hessian (i.e., $-\mathbf{I}$) in place of the usual Hessian (Jennrich and Sampson 1976). In this case, the equation describing the iteration used in Fisher's Scoring Method becomes

$$\hat{\theta}_{l+1} = \hat{\theta}_l + \mathbf{I}^{-1}(\hat{\theta}_l) \nabla l(\hat{\theta}_l). \quad (10)$$

where $\hat{\theta}_{l+1}$ is the maximum likelihood estimator of θ on iteration $l+1$, $\hat{\theta}_l$ is the maximum likelihood estimator of θ on iteration l , $\mathbf{I}^{-1}(\hat{\theta}_l)$ is the inverse of the Fisher Information Matrix evaluated at $\hat{\theta}_l$, and $\nabla l(\hat{\theta}_l)$ is the gradient or score function, which represents the first derivative of the log-likelihood function evaluated at $\hat{\theta}_l$. The algorithm proceeds by making a first initial guess at the MLE, then iterating equation (10) until the estimate changes by no more than a given error tolerance (e.g., 10^{-5}). As an initial guess, we use the sample mean of the single-year estimate of RRS given by equation (4).

Bootstrap Simulation

As an alternative approach to estimating the precision of $\hat{\theta}$, bootstrap simulation is used. Additionally, this approach yields an estimate of accuracy (bias). Bootstrap estimates of precision and accuracy do not rely on asymptotic theory as in the previous sections. That is, bootstrap estimates of precision and bias will work with small sample sizes (n). The bootstrap method proceeds by drawing NSIM random samples from the probability distribution of x given by equation (1), then calculating the MLE of RRS for each bootstrap sample. This yields NSIM replications of the MLE, denoted by $\hat{\theta}_1^*, \hat{\theta}_2^*, \dots, \hat{\theta}_{NSIM}^*$. The bootstrap estimate of the standard error of the MLE of the proportion of hatchery-origin spawners is then equal to the square root of the sample variance of the bootstrap replications:

$$SE^*(\hat{\theta}) = \sqrt{\sum_{k=1}^{NSIM} \frac{(\hat{\theta}_k^* - \bar{\hat{\theta}}^*)^2}{NSIM - 1}}, \quad (11)$$

where $\bar{\hat{\theta}}^*$ is the sample mean of the bootstrap replications. The coefficient of variation of $\hat{\theta}$ is

$$CV^*(\hat{\theta}) = \frac{SE^*(\hat{\theta})}{\theta}. \quad (12)$$

The relative bias is calculated as

$$bias^*(\hat{\theta}) = \frac{\bar{\hat{\theta}}^* - \theta}{\theta}. \quad (13)$$

Estimation of log(RRS)

The estimation outlined above was for the relative reproductive success RRS itself. The webtool RRS focusses on log(RRS), not on RSS. However, it is a simple matter to calculate the MLE of $\delta = \log(\text{RRS})$ and its variance using the MLE and variance of RRS itself. Using maximum likelihood theory, it is easily demonstrated that

$$\hat{\delta} = \log(\hat{\theta}). \quad (14)$$

The variance of log(RRS) is found using the Delta method (Seber 1982), which uses a Taylor series approximation to find the variance of a transformed random variable:

$$\text{var}(\hat{\delta}) = \text{var}(\log(\hat{\theta})) = \frac{\text{var}(\hat{\theta})}{\theta^2}. \quad (15)$$

When using bootstrap simulations to estimate SE, CV, and relative bias, simply substitute δ for θ in the equations (11)-(13).

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APPENDIX A. NAMES OF VARIABLES

Table A.1.—Variables.

| R code | Mathematical derivation | Definition |
|------------|-------------------------|--|
| Sw | $S_{W,t}$ | Number of wild-born female spawners (one for each year t). |
| Sh | $S_{H,t}$ | Number of hatchery-born female spawners (one for each year t). |
| n | n_t | The sample size of progeny that are genotyped and assigned back to spawning females (one number for each year t). |
| nw | x_t | Number of sampled progeny that are assigned to a wild-born mother (one for each year t). |
| nh | $n_t - x_t$ | Number of sampled progeny that are assigned to a hatchery-born mother (one for each year t). |
| theta | θ | Relative reproductive success (RRS) of hatchery-origin spawners |
| delta | δ | The natural log of RRS |
| n.a. | $l(\theta)$ | Log-likelihood function of RRS |
| SE.delta | $SE(\hat{\delta})$ | Standard error of the estimate of $\log(\text{RRS})$ |
| CV.delta | $CV(\hat{\delta})$ | Coefficient of variation of the estimate of $\log(\text{RRS})$ |
| BIAS.delta | $bias^*(\hat{\delta})$ | Monte Carlo relative bias which is the bias divided by the true value of $\hat{\delta}$. |

APPENDIX B. R-CODE

Table B.1. R-code

```

#Program to estimate the relative reproductive success (RRS)
#of hatchery-origin spawners using multiple brood years.
#AUTHOR: Richard A. Hinrichsen, Ph.D.
#DATE: 9-29-2014
#FILE: rrs2e-9-29-2014.s
#input variables
#Sw number of wild-origin spawning females (one for each year)
#Sh number of hatchery-origin spawning females (one for each year)
#nw is the number of sampled progeny with a wild-born mother (one for each year)
#nh is the number of sampled progeny with a hatchery-born mother (one for each year)
#delta is log(RRS)

#top level function
rrs2e.main<-function(Sw=c(200,200),Sh=c(200,200),nw=c(444,111),nh=c(356,89),BOOT=FALSE,NSIM=1000){
  check.inputs(Sw,Sh,nw,nh,BOOT,NSIM)
  if(!BOOT){res<-rrs2e(Sw=Sw,Sh=Sh,nw=nw,nh=nh)}
  if(BOOT){res<-rrs2e.boot(Sw=Sw,Sh=Sh,nw=nw,nh=nh,NSIM)}
  final.res<-list(BOOT=res$BOOT,
    NSIM=res$NSIM,
    Sw=res$Sw,
    Sh=res$Sh,
    nw=res$nw,
    nh=res$nh,
    delta=res$delta,
    SE.delta=res$SE.delta,
    CV.delta=res$CV.delta,
    BIAS.delta=res$BIAS.delta)
  return(final.res)
}

#check that inputs are valid
check.inputs<-function(Sw,Sh,nw,nh,BOOT,NSIM){
  if(!is.logical(BOOT))stop("BOOT must be TRUE or FALSE")
  if(BOOT){
    if(floor(NSIM)!=NSIM){stop("NSIM must be a positive integer")}
    if(NSIM<=0){stop("NSIM must be a positive integer")}}
  #check dimension of inputs
  k1<-length(Sw);k2<-length(Sh);k3<-length(nw);k4<-length(nh)
  mytest<-abs(k1-k2)+abs(k2-k3)+abs(k3-k4)
  if(mytest>0) stop("dimensions of Sw, Sh, nw, and nh must match")
  if(!is.numeric(Sw)){stop("Sw must be a number")}
  if(!is.numeric(Sh)){stop("Sh must be a number")}
  if(!is.numeric(nw)){stop("nw must be a number")}
  if(!is.numeric(nh)){stop("nh must be a number")}
  if(sum(floor(nw)-nw)){stop("Each nw must be a positive integer")}
  if(sum(nw<=0)){stop("Each nw must be a positive integer")}
  if(sum(floor(nh)-nh)){stop("Each nh must be a positive integer")}
  if(sum(nh<=0)){stop("Each nh must be a positive integer")}
  if(sum(floor(Sw)-Sw)){stop("Each Sw must be a positive integer")}
  if(sum(Sw<=0)){stop("Each Sw must be a positive integer")}

```

```

if(sum(floor(Sh)-Sh)){stop("Each Sh must be a positive integer")}
if(sum(Sh<=0)){stop("Each Sh must be a positive integer")}
return(NULL)
}

```

```

#This uses theoretical formulas from Hinrichsen (2003)

```

```

rrs2e<-function(Sw,Sh,nw,nh){
  n<-nw+nh
  res<-get.estimate(Sw,Sh,nw,nh)
  delta<-res$delta
  theta<-exp(delta)
  INF<-sum((n*Sh*Sw)/(theta*(Sw+Sh*theta)^2))
  thetavar<-1/INF
  deltavar<-thetavar/(theta*theta)
  se<-sqrt(deltavar)
  myres<-list(BOOT=FALSE,
    NSIM=NA,
    Sw=Sw,
    Sh=Sh,
    nw=nw,
    nh=nh,
    delta=delta,
    SE.delta=se,
    CV.delta=se/delta,
    BIAS.delta=NA)
  return(myres)
}

```

```

#return MLE of delta and its SE

```

```

#use Fisher's Scoring Method

```

```

get.estimate<-function(Sw,Sh,nw,nh){
  NTRIAL<-100
  Rw<-nw
  n<-nw+nh
  theta<-mean(Sw*(n-Rw)/(Rw*Sh))
  tol<-1.e-5

```

```

for(ii in 1:NTRIAL){
  INF<-sum((n*Sh*Sw)/(theta*(Sw+Sh*theta)^2))
  df<-sum((n-Rw)/theta-n*Sh/(Sw+Sh*theta))
  delx<-(1/INF)*df
  theta<-theta+delx
  errx<-sum(abs(delx))/abs(theta)
  if(errx<=tol)break
}
if(ii==NTRIAL){
  warning("maximum number of iterations was reached")
  return(list(delta=NA,se=NA))
}
delta<-log(theta)
thetavar<-1/INF
deltavar<-thetavar/(theta*theta)
se<-sqrt(deltavar)
return(list(delta=delta,se=se))

```

```

}

#calculate SE using bootstrap simulation
rrs2e.boot<-function(NSIM,Sw,Sh,nw,nh){
  n<-nw+nh
  res<-get.estimate(Sw,Sh,nw,nh)
  delta<-res$delta
  theta<-exp(delta)
  prob<-Sw/(Sw+Sh*theta)
  nprob<-length(prob)
  Rw<-rep(NA,nprob)
  deltas<-rep(NA,NSIM)
  ses<-rep(NA,NSIM)

  for(ii in 1:NSIM){
    Rw<-rep(NA,nprob)
    for(jj in 1:nprob){
      Rw[jj]<-rbinom(n=1,size=n[jj],prob=prob[jj])
    }
    res<-get.estimate(Sw,Sh,Rw,n-Rw)
    deltas[ii]<-res$delta
    ses[ii]<-res$se
  }
  se<-sqrt(var(deltas,na.rm=T))
  mymean<-mean(deltas,na.rm=T)
  BIAS.delta<-(mymean-delta)/delta
  myres<-list(BOOT=TRUE,
    NSIM=NSIM,
    Sw=Sw,
    Sh=Sh,
    nw=nw,
    nh=nh,
    delta=delta,
    SE.delta=se,
    CV.delta=se/delta,
    BIAS.delta=BIAS.delta)
  return(myres)
}

```
