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Article

Evaluating the Ryman–Laikre effect for marine stock enhancement and aquaculture

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Abstract

The Ryman–Laikre (R-L) effect is an increase in inbreeding and a reduction in total effective population size (N_{eT}) in a combined captive–wild system, which arises when a few captive parents produce large numbers of offspring. To facilitate evaluation of the R-L effect for scenarios that are relevant to marine stock enhancement and aquaculture, we extended the original R-L formula to explicitly account for several key factors that determine N_{eT}, including the numbers of captive and wild adults, the ratio of captive to wild N_e/N (β), productivity of captive and wild breeders, and removal of individuals from the wild for captive breeding. We show how to provide quantitative answers to questions such as: What scenarios lead to no loss of effective size? What is the maximum effective size that can be achieved? and What scenarios insure that N_{eT} will be no smaller than a specified value? Important results include the following: (1) For large marine populations, the value of β becomes increasingly important as the captive contribution increases. Captive propagation will sharply reduce N_{eT} unless the captive contribution is very small or β is very large ($\sim 10^3$ or higher). (2) Very large values of β are only possible if wild N_e/N is tiny. Therefore, large wild populations undergoing captive enhancement at even modest levels will suffer major reductions in effective size unless wild N_e is a tiny fraction of the census size (about 10^{-4} or lower).

Key words. captive breeding, effective population size, inbreeding, genetic drift.

Introduction

Each year, staggering numbers of captively reared individuals are intentionally released into the wild, where they can interact with (and potentially interbreed with) wild populations. These programs, which have varying goals but typically seek to enhance harvest opportunities, cover a wide range of taxa and are particularly widespread in the fields of fisheries, forestry, and wildlife management (Laikre et al. 2010). Unintentional escape into the wild of individuals or gametes from aquaculture and agriculture creates additional opportunities for genetic exchange between captive and wild populations. In the marine environment, juvenile-release, stock enhancement programs exist for hundreds of species around the world (Bartley et al. 2004; Lorenzen et al. 2013), and closed aquaculture operations for marine species are increasing rapidly (FAO 2014).

Genetic and ecological risks that captive individuals pose for natural populations have been well described theoretically and well documented empirically. General discussions can be found in: Allendorf and Ryman (1987), Hindar et al. (1991), Waples (1991), Busack and Currens (1995), Campton (1995), Waples (1999), Ford (2002), Brannon et al. (2004), Waples and Drake (2004), Naish et al. (2007), Fraser (2008), Araki and Schmid (2010), and Waples et al. (2012). Genetic risks are of 3 general types: (1) loss of diversity within populations; (2) loss of diversity among populations; and (3) loss of fitness. This study focuses on loss of within-population diversity.

In a classic paper, Ryman and Laikre (1991) were the first to explain how selective enhancement of a portion of a wild gene pool can reduce effective population size (N_e), leading to increased rates

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of genetic drift and more rapid loss of genetic diversity, thereby limiting evolutionary potential. In general, the purpose of captive breeding is to bypass high mortality that typically occurs in early life stages in the wild. The common scenario that motivated Ryman and Laikre's study can be summarized as follows:

- A small number of individuals are removed from the wild population to use for captive breeding.
- The captive breeders produce more offspring per parent than do individuals reproducing in wild.
- If the program is successful, offspring of the relatively few captive parents can make up a substantial fraction of the next generation.
- These offspring of captive parents will all be closely related, and when they interbreed the next generation their offspring will be inbred. This increased level of inbreeding will reduce overall N_e and can lead directly to reduced fitness of inbred offspring.
- The reduction in overall N_e in the captive–wild system due to selective enhancement of part of the gene pool has been termed the Ryman–Laikre (R-L) effect. It can be thought of as a kind of artificial bottleneck, because a large fraction of all the genes that pass from one generation to the next must be funneled through the few captive breeders.

The R-L effect has been evaluated in numerous studies, but some key gaps remain in our understanding of this important phenomenon. First, many of the analyses of this phenomenon have involved artificial propagation of relatively small natural populations, particularly of salmon (e.g., Waples and Do 1994; Nomura 1999; Hedrick et al. 2000; Moyer et al. 2007; Araki et al. 2007; Christie et al. 2012). Relatively less attention has been directed at evaluating the R-L effect in marine species, which typically have very large populations and are the focus of this special column (but see Tringali and Bert 1998; Hedgecock and Coykendall 2007; Gold et al. 2008; Kitada et al. 2009; and Gruenthal and Drawbridge 2012 for some notable exceptions). Second, a variety of factors can influence the nature and magnitude of the R-L effect, and to date no study has integrated all of these factors into a single quantitative analysis.

In this study, we focus on the practical implications of the R-L effect for the types of artificial propagation programs that are typically found with marine stock enhancement and marine aquaculture, and for the wild populations they are associated with. We use 2 different metrics: (1) the magnitude of N_e in the captive–wild population as a whole, after accounting for any R-L effect, and (2) the ratio of treatment N_e (after accounting for effects of captive breeding) to control N_e (for the wild population without captive breeding). We begin by deriving extensions to the basic Ryman–Laikre equation that explicitly account for: (1) size of the captive and wild populations; (2) removal of wild individuals for captive breeding; (3) the N_e/N ratio in captive and wild breeders; and (4) adult–adult replacement rates of captive and wild breeders, which determine the proportional representation of captive progeny in the offspring generation. We show how the modified equations can be used to obtain answers to questions that are commonly of management/conservation interest, including:

- What scenarios will ensure that overall N_e is not reduced by the R-L effect?
- What scenarios will ensure that the ratio of treatment to control N_e is no smaller than a specified value?
- What scenarios will ensure that, even if overall N_e is reduced by the R-L effect, it remains above some target level?
- Under what scenarios can captive rearing actually increase overall N_e, and if so what is the maximum increase that can be achieved?

We illustrate the new results with examples related to marine stock enhancement. We also briefly summarize what managers need to know about the R-L effect as it applies to marine species and how they can minimize the adverse consequences of reduced genetic diversity due to this effect. Finally, we close with some caveats about potentially important factors that are not considered here (nor in most other evaluations of the R-L effect), including effects of overlapping generations, multiple generations of captive breeding, and metapopulation structure.

Background and Analysis

Ryman and Laikre (1991) provided the following expression for effective population size in a captive–wild system:

$$N_{e(T)} = \frac{1}{\dfrac{x^2}{N_{e(C)}} + \dfrac{(1-x)^2}{N_{e(W)}}}, \qquad (1)$$

where $N_{e(T)}$ = total effective size of the cultured-wild system as a whole, $N_{e(C)}$ = effective size of the individuals reproducing in captivity, $N_{e(W)}$ = effective size of the individuals reproducing in the wild, x = the fraction of spawners in the offspring generation that were produced in captivity, and $1–x$ = the fraction of spawners in the offspring generation that were produced in the wild. This equation applies to the inbreeding effective size for a single generation of captive reproduction in a species with discrete generations.

Equation 1 is elegantly simple and has been very useful in many applications. However, it does not explicitly capture 2 features of the problem that can have an important influence on the results. First, overall effective size can be very sensitive to ratios of N_e to N (adult census size) in the wild and captive components of the population, and this is particularly true when N_e/N in the wild is very low, as it might be in at least some marine populations. For example, although captive breeding can never increase $N_{e(T)}$ if the N_e/N ratio is the same in the captive and wild components, that is not true if N_e/N is higher in captivity.

To explicitly account for this, we denote separate N_e/N ratios in the wild and in captivity as α_W and α_C, respectively. It is also convenient to define the proportional constant $\beta = \alpha_C/\alpha_W$, so that the ratio in captivity can be expressed as a proportion of that in the wild: $\alpha_C = \beta\alpha_W$. This allows the following substitutions in Equation 1: $N_{e(W)} = \alpha_W N_W$ and $N_{e(C)} = \beta\alpha_W N_C$, leading to:

$$N_{e(T)} = \frac{1}{\dfrac{x^2}{\beta\alpha_W N_C} + \dfrac{(1-x)^2}{\alpha_W N_W}} = \frac{\alpha_W}{\dfrac{x^2}{\beta N_C} + \dfrac{(1-x)^2}{N_W}}. \qquad (2)$$

The second issue, which is not always considered in evaluations of the Ryman–Laikre effect, is that bringing some individuals into captivity for breeding purposes reduces both N_W and $N_{e(W)}$ in the wild. That is, N_W and $N_{e(W)}$ are not independent of N_C. If we let N_W and $N_{e(W)}$ represent the census and effective size of the wild population without any removal for captive breeding, then realized values (denoted with an *) that account for such removals are $N_W{}^* = N_W – N_C$ and $N_{e(W)}{}^* = \alpha_W(N_W – N_C)$. Equations 1 and 2 will overestimate $N_{e(T)}$ (and hence underestimate the magnitude of the Ryman–Laikre effect) if N_W or $N_{e(W)}$ are used instead of $N_W{}^*$ and

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$N_{e(W)}{}^*$. Replacing N_W in Equation 2 with $N_W{}^*$ and substituting as above produces

$$N_{e(T)} = \frac{\alpha_W}{\dfrac{x^2}{\beta N_C} + \dfrac{(1-x)^2}{(N_W - N_C)}}. \tag{3}$$

The final key parameter to consider is the proportional contribution of captive individuals, x, which can be defined as $N_C{}'/(N_C{}'+N_W{}')$, where $N_C{}'$ ($N_W{}'$) is the number of captive (wild) adult breeders in the next generation. Similarly, $1-x = N_W{}'/(N_C{}'+N_W{}')$. We can also define adult–adult replacement rates of the captive and wild breeders as $\lambda_C = N_C{}'/N_C$ and $\lambda_W = N_W{}'/(N_W - N_C)$ so that $N_C{}' = \lambda_C N_C$ and $N_W{}' = \lambda_W(N_W - N_C)$. Finally, let $\phi = \lambda_C/\lambda_W =$ the ratio of the replacement rates for captive and wild breeders, so that the captive adult–adult replacement rate can be expressed as $\lambda_C = \phi\lambda_W$. Then $x = \phi\lambda_W N_C/(\phi\lambda_W N_C + \lambda_W(N_W - N_C))$ and $1-x = \lambda_W N_W/(\phi\lambda_W N_C + \lambda_W(N_W - N_C))$, and substituting into Equation 3 produces

$$\begin{aligned} N_{e(T)} &= \frac{\alpha_W}{\dfrac{\left[\dfrac{N_C{}'}{N_C{}'+N_W{}'}\right]^2}{\beta N_C} + \dfrac{\left[\dfrac{N_W{}'}{N_C{}'+N_W{}'}\right]^2}{N_W - N_C}} \\ &= \frac{\alpha_W}{\dfrac{\left[\dfrac{\phi\lambda_W N_C}{\phi\lambda_W N_C + \lambda_W(N_W - N_C)}\right]^2}{\beta N_C} + \dfrac{\left[\dfrac{\lambda_W N_W}{\phi\lambda_W N_C + \lambda_W(N_W - N_C)}\right]^2}{N_W - N_C}}. \end{aligned} \tag{4}$$

Note from Equations 2–4 that $N_{e(T)}$ is directly proportional to α_W. All else being equal, therefore, overall N_e is larger when the N_e/N ratio in the wild is larger.

The above equations allow one to calculate absolute values of $N_{e(T)}$, which can be useful in trying to ensure that overall effective size does not drop below some minimum threshold (see Tringali and Bert (1998) for an example of this type). In many cases, however, a more meaningful question is: How does the overall effective size (after accounting for captive breeding) compare to what it would have been if no propagation program had been implemented? To answer this question, it is necessary to consider the ratio $N_{e(T)}/N_{e(W)}$. Using the relationship $N_{e(W)} = \alpha_W N_W$ and substituting in Equation 4 leads to

$$\begin{aligned} \frac{N_{e(T)}}{N_{e(W)}} &= \frac{1}{\alpha_W N_W} \times \\ &\quad \frac{\alpha_W}{\dfrac{\left[\dfrac{\phi\lambda_W N_C}{\phi\lambda_W N_C + \lambda_W(N_W - N_C)}\right]^2}{\beta N_C} + \dfrac{\left[\dfrac{\lambda_W N_W}{\phi\lambda_W N_C + \lambda_W(N_W - N_C)}\right]^2}{N_W - N_C}} \\ &= \frac{1}{N_W\left[\dfrac{\left[\frac{\phi\lambda_W N_C}{\phi\lambda_W N_C+\lambda_W(N_W-N_C)}\right]^2}{\beta N_C} + \dfrac{\left[\frac{\lambda_W N_W}{\phi\lambda_W N_C+\lambda_W(N_W-N_C)}\right]^2}{N_W - N_C}\right]}. \end{aligned} \tag{5}$$

The ratio $N_{e(T)}/N_{e(W)}$ can be thought of as the ratio of effective sizes in the treatment and control populations. Equation 5 thus provides a quite general way to quantify the Ryman–Laikre effect for a program that lasts for a single generation.

This formulation shows that the ratio of treatment/control N_e does not depend separately on the wild and captive N_e/N ratios but only on their ratio, β. β appears in the denominator of the first term in the denominator of Equation 5. As β increases, the term $x^2/\beta N_C$ gets smaller, which means that the overall ratio $N_{e(T)}/N_{e(W)}$ gets larger. Therefore, all else being equal, a higher ratio of captive to wild N_e/N leads to a higher $N_{e(T)}/N_{e(W)}$. Furthermore, as the hatchery proportion x increases, the relative importance of the $x^2/\beta N_C$ term also increases, which means that the ratio of N_e/N in captive and wild populations becomes increasingly important for large programs.

Unlike the situation with β, which appears in only one term in Equations 2–5 and thus has predictable effects on results, $\phi =$ the ratio of the replacement rates for captive and wild breeders appears in both numerators and denominators of Equation 5, and as a consequence the direction of its effect varies with values of ϕ in relation to other parameters. Some special cases can be noted. If $\phi < 1$ (replacement rate of captive breeders is less than that of wild breeders), then overall effective size will always be less than that of the wild control, but the difference becomes increasingly small as β becomes increasingly large. If $\phi = 1$ (equal replacement rates of captive and wild breeders), then there is no enhancement of total population size, and the ratio $N_{e(T)}/N_{e(W)}$ follows a simple pattern that depends on β: overall effective population size declines if $\beta < 1$, remains unchanged if $\beta = 1$, and increases if $\beta > 1$. We are more interested in situations where captive productivity is higher than that in the wild, in which case $\phi > 1$. In this case, behavior of $N_{e(T)}/N_{e(W)}$ depends in a complex way on β and ϕ. To make these analyses more tractable, we take advantage of some simplifications that are reasonable for many, if not most, captive programs involving marine species.

First, the correction to realized $N_W{}^*$ and $N_{e(W)}{}^*$ for removing broodstock is particularly important in conservation applications, where captive propagation is used to supplement a small wild population to reduce extinction risk. Many applications of the Ryman–Laikre model to real-world situations are of this type (e.g., Araki et al. 2007; Christie et al. 2012; Small et al. 2014; Waters et al. 2015). For most marine species, however, removing a small number of wild individuals for captive breeding has a negligible effect on $N_W{}^*$ and $N_{e(W)}{}^*$. Furthermore, many aquaculture operations obtain broodstock from domesticated sources that do not rely on wild capture. For these applications, therefore, we can consider that $N_W{}^* = N_W - N_C \approx N_W$. In that case, Equation 5 simplifies to

$$\frac{N_{e(T)}}{N_{e(W)}} \approx \frac{1}{N_W\left[\dfrac{\left[\dfrac{\phi\lambda_W N_C}{\phi\lambda_W N_C + \lambda_W N_W}\right]^2}{\beta N_C} + \dfrac{\left[\dfrac{\lambda_W N_W}{\phi\lambda_W N_C + \lambda_W N_W}\right]^2}{N_W}\right]}. \tag{6}$$

(Assumes $N_W \gg N_C$)

Similarly, if the captive program is not primarily for conservation, it is reasonable to assume that the wild population is relatively stable, in which case $N_W{}' = N_W$, $\lambda_W = 1$, $\phi = \lambda_C$, and Equation 6 simplifies to

$$\begin{aligned} \frac{N_{e(T)}}{N_{e(W)}} &\approx \frac{1}{N_W\left[\dfrac{\left[\dfrac{\lambda_C N_C}{\lambda_C N_C + N_W}\right]^2}{\beta N_C} + \dfrac{\left[\dfrac{N_W}{\lambda_C N_C + N_W}\right]^2}{N_W}\right]} \\ &= \frac{1}{\dfrac{N_W}{\beta N_C}\dfrac{\lambda_C{}^2 N_C{}^2}{[\lambda_C N_C + N_W]^2} + \dfrac{N_W{}^2}{[\lambda_C N_C + N_W]^2}} \\ &= \frac{1}{\dfrac{N_W}{[\lambda_C N_C + N_W]^2}\left[\dfrac{\lambda_C{}^2 N_C}{\beta} + N_W\right]}. \end{aligned} \tag{7}$$

(Assumes a stable wild population with $N_W \gg N_C$)

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Table 1. Formulas for computing some values of interest in evaluating the Ryman–Laikre effect

	$N_{e(W)}$ reduced by captive removal	No reduction for captive removal
x for which $N_{e(T)}/N_{e(W)} = 1$	$\dfrac{A + \sqrt{A + C - AC}}{A + C}$	$\dfrac{2}{1 + \dfrac{N_W}{\beta N_C}}$
x for which $N_{e(T)}/N_{e(W)} = R$	$\dfrac{A + \sqrt{A/R + C/R - AC}}{A + C}$	$\dfrac{1 + \sqrt{1 - (1 - \dfrac{1}{R})\left[1 + \dfrac{N_W}{\beta N_C}\right]}}{1 + \dfrac{N_W}{\beta N_C}}$
x for which $N_{e(T)}/N_{e(W)} =$ maximum	$\dfrac{1}{1 + \dfrac{N_W}{\beta N_C} - \dfrac{1}{\beta}}$	$\dfrac{1}{1 + \dfrac{N_W}{\beta N_C}}$
Maximum value of $N_{e(T)}/N_{e(W)}$	$1 + \dfrac{(\beta - 1)N_C}{N_W}$	$1 + \dfrac{\beta N_C}{N_W}$
x for which $N_{e(T)} = Y$	$\dfrac{D + \sqrt{D\alpha_W/Y + F\alpha_W/Y - DF}}{DF}$	$\dfrac{1 + \sqrt{\dfrac{N_W\alpha_W}{Y}[1 + C] - C}}{1 + \dfrac{N_W}{\beta N_C}}$

Formulas in the second column are for scenarios in which N_W and $N_{e(W)}$ are reduced by taking N_C individuals into captivity; formulas in the third column assume that captive breeding does not require removal of individuals from the wild population, or that such removals are a small enough fraction of the wild population that they can be ignored.

$A = N_W/(N_W - N_C)$; $C = N_W/(\beta N_C)$; $D = 1/(\beta N_C)$; $F = 1/(N_W - N_C)$; see Table 2 for other notation. R and Y represent values that might be chosen by a user as targets to meet or exceed.

Remembering that we are interested in the case where removal of N_C individuals for breeding is inconsequential for the wild population size, Equation 7 can be further simplified by assuming that $(\lambda_C N_C + N_W) \approx N_W$, in which case

$$\frac{N_{e(T)}}{N_{e(W)}} \approx \frac{1}{\dfrac{1}{N_W}\left[\dfrac{\lambda_C{}^2 N_C}{\beta} + N_W\right]}$$

$$= \frac{1}{\dfrac{\lambda_C{}^2 N_C}{\beta N_W} + 1}. \tag{8}$$

(Assumes a stable wild population with $N_W \gg \lambda_C N_C$)

We can see from Equation 8 that the reduction in $N_{e(T)}$ compared with the control is determined by the extent to which the term $\lambda_C{}^2 N_C/(\beta N_W)$ exceeds zero. If there is no program ($N_C = 0$) or captive progeny do not contribute to the next generation ($\lambda_C = 0$), this term is zero and there is no Ryman–Laikre effect. Note also that as β gets arbitrarily large, the term $\lambda_C{}^2 N_C/(\beta N_W)$ approaches zero and the Ryman–Laikre effect becomes very small. Realistically, captive N_e/N cannot be much higher than 0.1–0.5, so very large values of β are only possible when the N_e/N ratio in the wild population is tiny, as has been proposed for many marine species (reviewed by Hauser and Carvalho 2008).

At the other extreme, consider what happens when N_e/N ratios in the captive and wild populations are roughly comparable ($\beta \approx 1$). In that case, $N_{e(T)}/N_{e(W)}$ is approximated by $1/(1 + (\lambda_C{}^2 N_C)/N_W)$. Unless $\lambda_C{}^2 N_C$ is very small compared with N_W, the reduction in $N_{e(T)}$ can be substantial. This formulation also highlights the contrasting effects of β and λ_C on the Ryman–Laikre effect. For any given values of N_W and N_C, the magnitude of the R-L effect depends on the ratio $\lambda_C{}^2/\beta$, with high values of captive productivity increasing the effect and high relative values of the captive N_e/N ratio reducing it.

These general equations also can be modified to give expressions for some quantities that are commonly of interest in evaluating the Ryman–Laikre effect. These expressions, which are shown in Table 1 and explained in the Supporting Information (available in Supplementary Material), answer questions such as: What values of x produce $N_{e(T)}/N_{e(W)}$ ratios that are: (1) equal to 1.0 (indicating no loss of effective size)? (2) equal to a specified value R? (3) the maximum possible, given the parameters involved? What is the maximum possible value of $N_{e(T)}/N_{e(W)}$? and What values of x produce $N_{e(T)}$ values equal to a specified effective population size Y?

Examples

Marine stock enhancement

The Ryman–Laikre equation was originally developed to analyze a situation in which captive individuals are intentionally released into the wild, so we focus first on marine stock enhancement and take up aquaculture (for which captive–wild interactions typically occur only as the result of unintentional escapes) in the next section.

We illustrate the above results with 3 generic scenarios, all of which assume a stable wild population in the absence of a captive program ($\lambda_W = 1$). Scenario I (for 'Scenarios', see Supplementary Table A1) mimics a supplementation program for a small local population and is typical of many applications of the R-L effect to salmon hatchery programs. This scenario used fixed values of $N_W = 100$, $N_C = 50$, and $\alpha_C = 0.3$ and allowed α_W to vary from 0.05 to 0.5 (producing β values ranging from 0.6 to 6), whereas λ_C varied from 0.1 to 64 (producing values of x in the range 0.09–0.98). Scenario II models a small enhancement program ($N_C = 20$) for a moderately sized ($N_W = 1{,}000$) local marine population. This scenario used an optimistic $\alpha_C = 1.0$ and allowed α_W to vary from 0.05 to 1 (producing $\beta = 1$–20), whereas λ_C again varied from 0.1 to 64 (producing $x = 0.002$–0.57). Scenario III models a typical marine enhancement program ($N_C = 100$) for a large ($N_W = 10^6$) marine population. This scenario fixed α_C at 0.1 and considered a wide range of values for α_W (0.5–10^{-6}, so $\beta = 0.2$–10^5) and λ_C (10–10^5, so $x = 0.001$–0.91).

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Table 2. Notation used in this study

N_W	Adult census size of the wild population, before effects of captive breeding
N_C	Number of adults taken from wild for captive breeding
$N_W{}^*$	Adult census size of the wild population after accounting for removal of individuals for captive breeding ($N_W{}^* = N_W – N_C$)
α_W	Ratio of effective size to census size in the wild population
$N_{e(W)}$	Effective population size in the wild, before effects of captive breeding ($N_{e(W)}=\alpha_W N_W$); also referred to as N_e(control)
$N_{e(W)}{}^*$	Realized effective size of the wild component, after accounting for removal of individuals for captive breeding ($N_{e(W)}{}^*=\alpha_W(N_W–N_C)$)
α_C	Ratio of effective size to census size in the captive population
$N_{e(C)}$	Effective size of the captive component ($N_{e(C)}=\alpha_C N_C$)
$N_{e(T)}$	Effective size of the combined population, which includes offspring from both wild and captive parents (see Equation 3); also referred to as N_e(treatment)
$N_{e(T)}/N_{e(W)}$	Effective size of the combined population as a fraction of the effective size of the wild population without captive breeding (see Equation 5; this can be considered to be the ratio of N_e (treatment)/N_e (control))
β	Ratio of N_e/N in captive and wild components ($\beta = \alpha_C/\alpha_W$, so $\alpha_C = \beta\alpha_W$)
N_C’	The number of adult breeders in the next generation produced by the N_C captive breeders in the current generation
λ_C	Adult–adult replacement rate of the captive population ($\lambda_C = N_C$’$/N_C$)
N_W’	The number of adult breeders in the next generation produced by the N_W wild breeders in the current generation
λ_W	Adult–adult replacement rate of the wild population ($\lambda_W = N_W$’$/(N_W–N_C)$)
ϕ	Ratio of adult–adult replacement rates of the captive and wild breeders ($\phi = \lambda_C/\lambda_W$)
x	Fraction of the total adult population in the offspring generation derived from captive parents ($x = N_C$’$/(N_C$’$+N_W$’$)$)
$1–x$	Fraction of the total adult population in the offspring generation derived from wild parents ($1–x = N_W$’$/(N_C$’$+N_W$’$)$)

First, we evaluated robustness of the approximations in Equations 6–8 by conducting a sensitivity analysis. For each parameter combination in each scenario, we calculated $N_{e(T)}/N_{e(W)}$ using the exact formula (Equation 5) and the approximations in Equations 7 and 8. As expected, results (Supplementary Table A1) show that failure of the approximations in Equations 7 and 8 to account for removal of broodstock from the wild substantially overestimated $N_{e(T)}/N_{e(W)}$ in Scenario I, in which half the wild individuals were actually brought into captivity. However, Equation 7 produced results that were only about 2% higher than the true values for Scenario II and were indistinguishable from those of Equation 5 for Scenario III. Therefore, this approximation works well in the scenarios that meet the assumption that $N_W \gg N_C$. Equation 8 further assumes that N_W is much larger than the product $\lambda_C N_C$, and if λ_C is large enough, this assumption can fail even if N_C is small compared with N_W. This situation occurred in Scenario III, where N_W is 4 orders of magnitude larger than N_C: when λ_C was 1,000, Equation 8 underestimated $N_{e(T)}/N_{e(W)}$ by 27% (Supplementary Table A1). Notably, this level of adult–adult replacement was sufficient only to bring the relative hatchery contribution to 9%; even higher captive productivities are required to make more substantial contributions from small captive programs to large marine populations. Results in Supplementary Table A1 demonstrate that Equation 8 is not a reliable quantitative predictor of $N_{e(T)}/N_{e(W)}$ for highly productive captive programs. Nevertheless, the simple relationship illustrated in this equation can still be useful for heuristic purposes to illustrate the relative influence of different key parameters.

Situations similar to Scenario I have been well studied by others, so here we only provide a brief treatment and instead focus on the other scenarios, which are more applicable to marine species. Figure 1A is derived from the original Ryman and Laikre (1991) equation and is being used for evaluating potential R-L effects in a wide range of supplementation programs for Atlantic salmon in Norway. The colored section defines the parameter space that results in $N_{e(T)}/N_{e(W)} \geq 1$, hence no reduction (and perhaps a slight gain) in overall N_e. The area to the upper left (above the red line) is the zone in which the R-L effect occurs, and the area in the lower right (below the green line) is the zone in which the contribution of captive individuals to the overall population is relatively small. The black circle represents one possible outcome involving a reduction in overall N_e that potentially could be improved by taking management actions indicated by the black arrows.

One limitation of this traditional approach to evaluating the R-L effect is that Equation 1 does not provide an explicit way to evaluate the consequences of removing individuals from the wild for captive breeding, which generally is an important consideration in Scenario I programs. The example shown in Figure 1B is for Scenario I as described above and in Supplementary Table A1 and analyzed using Equation 3, which accounts for broodstock removal. In this contour plot, colors indicate values of $N_{e(T)}/N_{e(W)}$ associated with different combinations of the captive contribution (x) and the ratio of N_e/N in captive and wild breeders (β). In this scenario, half of the $N_W = 100$ wild individuals are taken for captive breeding, so $N_C = N_{W*} = 50$. If N_e/N in captivity and the wild are the same ($\beta = 1$), then $N_{e(T)}/N_{e(W)} = 1$ when the captive contribution is 50% ($x = 0.5$). If N_e/N in captivity is greater than in the wild ($\beta > 1$), then $N_{e(T)}/N_{e(W)} = 1$ can be achieved with higher captive contributions (dashed line). As β increases, the maximum possible $N_{e(T)}$ that can be achieved (calculated using the formula in Table 1) also is associated with a higher captive contribution (solid line). The red circle in Figure 1B represents a hypothetical program that would lead to a sharp reduction in effective size. By reducing the proportional hatchery contribution and/or increasing captive N_e/N compared with the wild (white arrow), managers could produce a better result with $N_{e(T)}/N_{e(W)} \geq 1$.

Scenario II involves a small-scale captive program ($N_C = 2\%$ of N_W), for which it is assumed that N_e/N in captivity is no smaller (and up to 20x larger) than wild N_e/N. If N_e/N in captivity and the wild are the same ($\beta = 1$), then $N_{e(T)}/N_{e(W)}$ reaches its maximum value (1.0) when $x = N_C/N_W = 2\%$ and is < 1 for all other hatchery fractions. But if N_e/N is higher in the captive breeders, then values of $N_{e(T)}/N_{e(W)} > 1$ are possible (Figure 2). Normally, if the relative captive contribution becomes large compared with the ratio N_C/N_W, $N_{e(T)}/N_{e(W)}$ declines. However, high values of β can offset this, at least to some extent. For

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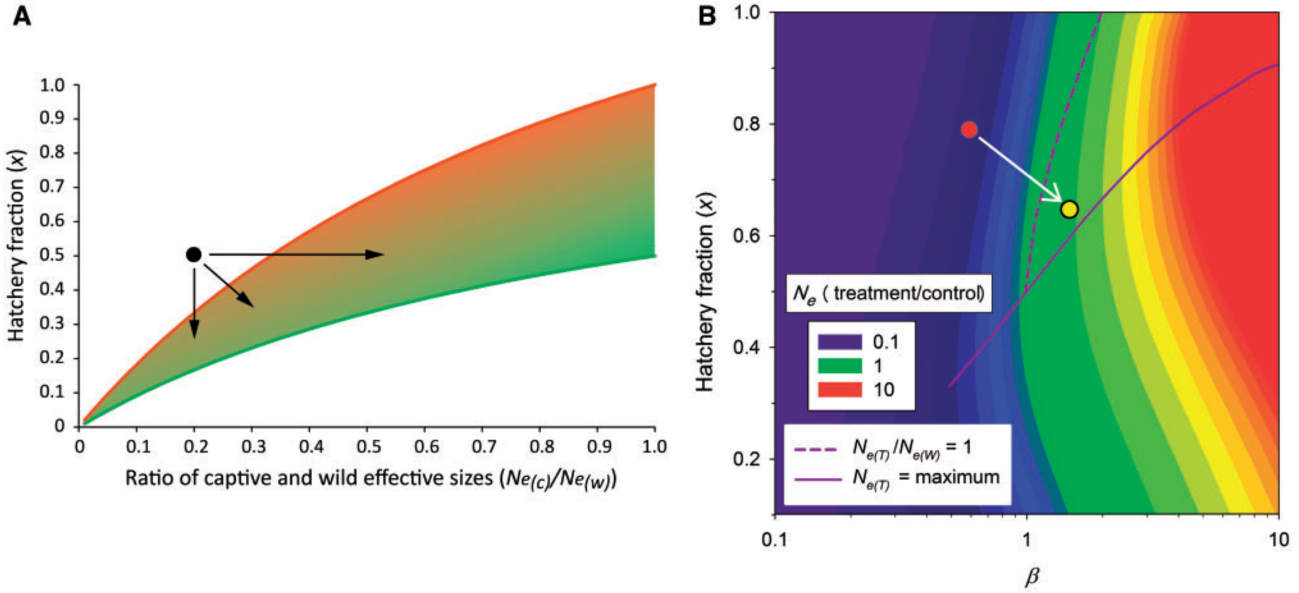

Figure 1. A. A traditional way (based on the parameters in Equation 1) to evaluate the Ryman–Laikre effect for an Atlantic salmon supplementation program (illustrative of Scenario I in the text). The colored parameter space is bounded by the green line (which shows combinations that produce the maximum N_e that can be achieved with stocking) and the red line (which shows combinations for which $N_{e(T)}/N_{e(W)} = 1$). The black circle represents one stocking scenario that leads to an overall reduction in effective size, and the black arrows illustrate ways to improve the result by reducing the number of stocked fish, increasing the number of captive breeders, or both. This figure does not account for removal of wild individuals for captive breeding. B. A contour-plot method (based on Equation 3) to depict the Ryman–Laikre effect for a supplementation program illustrative of Scenario I in the text. The contours show the value of $N_{e(T)}/N_{e(W)}$ (the ratio of overall N_e in the treatment to the control) as a function of the proportional captive contribution (x) and the ratio of N_e/N in captive and wild breeders (β). The dashed line is the prediction (from the equation in the left column in Table 1) of the combinations of β and x values that will produce $N_{e(T)}/N_{e(W)} = 1$; the solid line depicts the x value that will produce the maximum $N_{e(T)}$ for each value of β. Fixed values assumed in this example are $N_W = 100$, $N_C = 50$, $\alpha_C = 0.3$: wild N before supplementation $= 100$, 50 fish are removed for captive breeding, and wild $N_e/N = 0.3$ The red circle represents one stocking scenario that leads to an overall reduction in effective size, and the arrow illustrate a way to improve the result by reducing the number of stocked fish and increasing N_e/N in captivity. This figure accounts for removal of wild individuals for captive breeding.

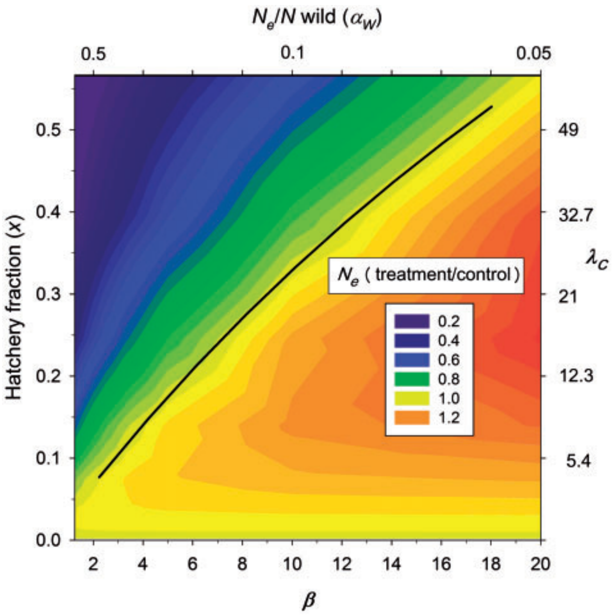

Figure 2. Contour plot showing values of $N_{e(T)}/N_{e(W)}$ (N_e treatment/control) for Scenario II, as a function of proportional captive contribution (x) and the ratio of N_e/N in captive and wild breeders (β). Corresponding values of wild N_e/N (α_W) and adult–adult replacement rate of captive breeders (λ_C) are also shown. Fixed values: $N_C = 20$, $N_W = 1{,}000$, $\alpha_C = 1.0$, and $\lambda_W = 1$. The black line is the prediction (from the equation in Table 1) of the combinations of β and x values that will produce $N_{e(T)}/N_{e(W)} = 1$, given $N_W/N_C = 50$.

example, in this scenario with $N_C/N_W = 0.02$, even with the captive contribution as high as 50%, overall N_e can still be as high or higher than in the control wild population, provided that captive N_e/N is about 16 or more times the N_e/N ratio in the wild (Figure 2).

How can one identify conditions under which the Ryman–Laikre effect is minimal (i.e., $N_{e(T)}/N_{e(W)} \approx 1$)? In Figure 2, those conditions are graphically described by the narrow yellow band that extends from lower left (x near 0, β near 1) to upper right ($x > 0.5$, $\beta \approx 20$). It is also possible to describe those conditions analytically using results in Table 1. Because the captive program removes only $N_C/N_W = 2\%$ of the wild population for broodstock, the expression in the last column of the first row in Table 1 $[2/(1 + (N_W/N_C)/\beta)]$ will be a good approximation to the value of x for which $N_{e(T)}/N_{e(W)} = 1$. This produces $x = 2/(1 + (1000/20)/\beta) = 2/(1 + 50/\beta)$. The solid black line in Figure 2 plots the values that satisfy this relationship; it is a good predictor of the conditions necessary to satisfy $N_{e(T)}/N_{e(W)} = 1$, with the slight offset due to the fact that we have ignored the removal of individuals for broodstock. An exact result can be obtained by applying the more complicated formula in column 2 of Table 1. For example, if we are interested in results for $\beta = 10$ (effective:census size ratio in captivity 10 times as large as in the wild, which in this example is equivalent to assuming that the ratio in the wild is $\alpha_W = 0.1$), the exact formula shows that $N_{e(T)}/N_{e(W)} = 1$ can be achieved if $x = 0.329$; application of the approximation in column 3 of Table 1 estimates the value of x as $2/(1 + 5) = 0.333$. It is interesting to note that if $N_W \gg N_C$, so that removal for captive propagation can be ignored, the value of x that will produce the maximum value of $N_{e(T)}/N_{e(W)}$ is exactly half of the hatchery fraction that produces

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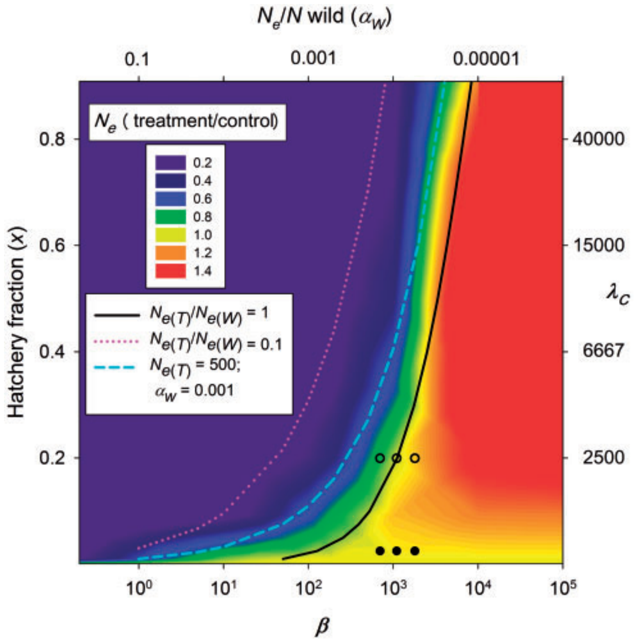

Figure 3. As in Figure 2, but for Scenario III with $N_C = 100$, $N_W = 10^6$, $\alpha_C = 0.1$, and $\lambda_W = 1$. Note the log scale on the x axis. The 3 lines depict relationships described by formulas in Table 1. The black line is combinations of β and x values that will produce $N_{e(T)}/N_{e(W)} = 1$, given $N_W/N_C = 10^4$. The pink dotted line is combinations of β and x values that will produce $N_{e(T)}/N_{e(W)} = 0.1$ (i.e., a 90% reduction in overall N_e). The cyan dashed line is combinations of β and x values that will produce $N_{e(T)} = 500$, assuming $\alpha_W = 10^{-3}$. The solid black circles represent a range of empirical estimates for enhancement programs of red drum (*Sciaenops ocellatus*); the open black circles are projected outcomes if the proportional captive contribution were increased from the current estimate of $x \approx 0.02$ to $x = 0.2$.

no change in effective size. For this example, the estimated maximum is achieved at $x = 0.164$ (the exact value from column 2 is 0.169), and this produces an estimated maximum value of $N_{e(T)}/N_{e(W)} = 1.2$ (the exact value from column 2 is 1.18). By rearranging the expression in Table 1 to solve for β in terms of the value of x that produces the maximum, we get $\beta = [(N_W/N_C) - 1]/(1/x - 1) = 23.99$. That is, under conditions as described in Scenario II, it is possible to increase effective size by almost 20% with appropriate selection of x, provided that the N_e/N ratio in captivity is more than 20 times as large as that in the wild.

Scenario III considers a common situation where a slightly larger captive program ($N_C = 100$) is used in conjunction with a large wild population ($N_W = 10^6$). Programs like this will result in more than trivial captive contributions only if the productivity of captive breeders is very high (in this case, adult–adult replacement rates of $\lambda_C = 10^3$–10^4). Such high captive productivity will dramatically lower overall N_e unless the ratio of captive to wild N_e/N (β) is comparably large (Figure 3). But very large values of β are only possible if the wild N_e/N ratio is very low. In Scenario III, wild N_e/N must be about 10^{-4} or lower for overall N_e to be maintained at its control level. Again, the analytical result from Equation 9 for $N_W/N_C = 10^4$ is a good predictor of the parameter space that produces $N_{e(T)}/N_{e(W)} \approx 1$ (black line in Figure 3). Note that a slight change in the wild N_e/N ratio has a large effect on the outcome. For example, if wild N_e/N is 10^{-4} instead of 10^{-5}, or 10^{-3} instead of 10^{-4}, the Ryman–Laikre effect leads to a severe reduction in overall N_e (dotted pink line in Figure 3, which identifies parameter combinations that lead to 90% reductions in N_e, using results in Table 1).

As noted earlier, one possible management goal is to design a captive program that will ensure that the overall effective size remains above a specific threshold. This can be done using the expressions in the last row of Table 1. The dashed cyan line in Figure 3 shows the parameter combinations required to produce $N_{e(T)} = 500$, which some consider a realistic target for conservation purposes. There are 2 important caveats, however. First, the cyan line falls to the left of the black "no R-L effect" line, which means that all parameter combinations here that produce $N_{e(T)} = 500$ also lead to reductions in effective size compared with what it would have been without the program. Second, as seen in Equation 3, $N_{e(T)}$ is directly proportional to α_W. The cyan line shown in Figure 3 assumes $\alpha_W = 10^{-3}$; it would be shifted to the left or right if the true wild N_e/N ratio were higher or lower, respectively.

Although Scenario III is hypothetical, the general features are similar to empirical data for red drum *Sciaenops ocellatus*, which for several decades has been the subject of enhancement efforts in the Gulf of Mexico and the Atlantic Ocean. For the Gulf population, Turner et al. (2002) estimated adult abundance as 3.4×10^6, and genetic methods applied to several geographic samples produced estimates of wild N_e/N in the range $\alpha_W = 5.4 \times 10^{-5}$ to 1.5×10^{-4}. Based on parentage analysis of progeny, Gold et al. (2008) estimated that the effective number of parents responsible for the red drum fingerlings released in 1 year was about 29–47, which would produce $\alpha_C \approx 0.5$–1. For a different red drum enhancement program in Florida, Tringali and Bert (1998) estimated that the contribution of captive progeny was 1.5–2.5% ($x = 0.015$–0.025). These results are plotted as black circles on Figure 3. Because estimated N_e/N in the wild is tiny, β is estimated to be very large, and with the very low estimated captive contribution there is no evidence for a significant R-L effect. This figure shows that the captive contribution could increase to about 10–20%, perhaps a little higher, before any appreciable reduction in N_e would be expected. However, the spread of the black circles along the x axis (which reflects the range of estimates of wild N_e/N) indicate how sensitive this conclusion is to the value of β. If x were increased to 0.2 and wild N_e/N actually is as small as the smallest estimate reported by Turner et al. (2002) (hence $\beta > 10^3$; right black open circle), then the net effect of the program on effective size would be neutral or perhaps even slightly positive. However, if wild N_e/N is actually bit larger, equal to the highest estimate by Turner et al. (2002) (hence $\beta < 10^3$; left black open circle), then increasing x to 0.2 would result in a reduction in overall N_e.

Marine aquaculture

All of the equations above and the expressions in Table 1 apply equally well to marine aquaculture, but a few things are important to note. First, many aquaculture programs use domesticated broodstock that has been selected for performance under captive conditions. These programs generally do not bring wild individuals into captivity each generation, in which case the adjustment for captive removal is not needed. Thus, all of the approximations that replace $N_W - N_C$ with N_W under the assumption that $N_W \gg N_C$ can be used for this type of program regardless whether N_C is small compared with N_W. Second, highly domesticated populations adapted to artificial conditions often have poor survival when they escape into the wild. Therefore, even if the number of escapees from aquaculture operations is large compared with the wild population, the number that survive to maturity and successfully reproduce can be much smaller, so x will not necessarily be large even if the number of escapes is substantial. Finally, if successful captive reproduction in the

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wild of aquaculture escapes is significant enough to produce a substantial R-L effect, the consequences likely would be dwarfed by other more serious concerns, for 2 reasons. First, substantial levels of interbreeding with domesticated aquaculture escapes can be expected to produce major reductions in fitness of the wild population, through outbreeding depression and/or loss of local adaptation (Edmands 1999; Baskett et al. 2013). Second, Equations 1–8 all assume a single population with 2 different environments for reproduction; however, many marine species, even those with high dispersal capability, show clear evidence of population structure (Hauser and Carvalho 2008; Nielsen et al. 2012). This means that a captive program can potentially affect multiple wild populations, with consequences not only for fitness but also among-population diversity (Glover et al. 2012).

Discussion

We want to emphasize that there is nothing wrong with Equation 1. Indeed, it has been used successfully in many practical applications. However, the 3 parameters in that formula (x, $N_{e(W)}$, and $N_{e(C)}$) are all complex functions of other key variables, so using only this formula can mask important factors that might be amenable to separate evaluation and perhaps management control. What we have done is to decompose the basic R-L equation into its component parts to facilitate evaluation of those other factors. Thus, the present study is meant to complement rather than replace evaluations that use the basic R-L equation.

Factors not considered here

Before discussing the results presented above, we want to touch on several important factors that have not been treated here in any detail.

First, all of the results presented here apply to a single generation of captive reproduction. Because a) the consequences for effective population size are cumulative over time, and b) few captive propagation programs are active for only one generation, overall effects could be much larger than indicated by Equations 1–8 or the expressions in Table 1. In recurrent programs, whether progeny of captive propagation subsequently become incorporated into the captive component can strongly affect results. Over the short term, marking captive progeny (e.g., with radio-frequency identification microtags) so they can be avoided during collection can be at least partially effective in reducing the consequences, but this might require nearly 100% marking and cannot realistically be effective across more than a few generations. Waples and Do (1994), Wang and Ryman (2001), and Duchesne and Bernatchez (2002) have evaluated the R-L effect under repetitive episodes of captive enhancement.

Second, the underlying model assumes discrete generations, but that assumption is violated for many (if not most) marine species subject to stock enhancement and/or aquaculture. Some efforts to account for age structure have been made for semelparous species like Pacific salmon (e.g., Waples and Do 1994), but little is known about how the R-L effect works in iteroparous species. This topic is an important area in need of research.

Third, the underlying model also assumes a single population that has captive and wild components. A method described by Tufto and Hindar (2003) could potentially be used to evaluate natural populations that are part of a metapopulation and which experience captive propagation.

Fourth, the original Equation 1 and our subsequent variations all apply to the inbreeding effective size. Ryman et al. (1995a) provided a comparable equation to calculate variance effective size and showed that in some circumstances it can produce different results. We think the inbreeding effective size is more generally useful, as it relates naturally to the number of adults in the parental generation and is a good predictor of the overall level of inbreeding that will occur in the population once random mating is achieved. However, results obtained by Waples and Do (1994) and Ryman et al. (1995a) emphasize the importance of considering what happens to total population size following selective enhancement. For example, if captive propagation substantially increases total abundance and population size remains large in subsequent generations, the total amount of inbreeding (related to inbreeding N_e) and the total amount of allele frequency change (related to variance N_e) can be less than they would have been without captive propagation—even when inbreeding N_e is reduced by the R-L effect during the captive generation.

Fifth, the proportional captive contribution (x) has a large effect on results, so it is important to remember that this represents the proportional genetic contribution of progeny of captive parents to the next generation. Direct genetic effects occur only if progeny of captive parents survive and reproduce in the wild. Therefore, if captive offspring are unlikely to survive to reproduce, or if they can be effectively targeted for selective removal (e.g., in fisheries that target captive offspring, or in mop-up operations following large aquaculture escape events), these realities should be factored into the calculation of x.

Finally, all of the treatment in this article is focused on consequences for effective population size. Captive propagation poses a much wider range of genetic and ecological risks for natural populations that should be considered in any overall risk assessment or conservation/management plan (for reviews that focus on marine species, see Waples and Drake 2004 and Waples et al. 2012).

General conclusions

To the best of our knowledge, Equations 2–8 are the first that integrate the most important factors that can influence the R-L effect into a single analysis. We show how to analytically solve for parameter combinations that will produce a desired N_e value, a desired ratio of N_e(treatment) to N_e(control), or the largest overall effective size. Heuristic insights gained from examination of these equations include the following:

- Overall N_e is directly proportional to the N_e/N ratio in the wild, so that ratio will place an upper limit on how large N_e(treatment) can be.
- The N_e/N ratio in captivity compared with the wild (β) is a key parameter. Three general scenarios are noteworthy:
  1. If $\beta < 1$, all parameter combinations reduce overall N_e.
  2. If $\beta = 1$, then overall N_e is reduced unless $x/(1-x) = N_{e(C)}/N_{e(W)}$.
  3. If $\beta > 1$, the higher N_e/N ratio in captivity can at least partially offset reductions in effective size due to other factors; depending on x, it is possible that the captive program can increase overall N_e. The importance of a high β increases as captive productivity (λ_C) and hence x increase.
- Reductions to N_W and $N_{e(W)}$ from removal of wild individuals for captive breeding have little effect as long as N_C is no more than a few percentage of N_W. However, for small wild populations it is essential to account for this removal.

Consequences for marine stock enhancement

Although some exceptions might occur for supplementation programs for at-risk species, most marine stock enhancement programs

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correspond roughly to our Scenario III, where the number of captive parents is a tiny fraction of those in the wild. This scenario is easier to evaluate because effects of captive removal can be ignored. Some important results include:

- When $N_W \gg N_C$, the value of β becomes increasingly important as the captive fraction increases. For example, in Figure 2, $N_{e(T)}/N_{e(W)}$ is largely insensitive to β in the range 1–20 for $x < 0.1$, but for $x = 0.2$ or higher, β determines whether the net result is a substantial reduction, little change, or an increase in $N_{e(T)}/N_{e(W)}$.
- Unless x is close to zero, captive propagation will sharply reduce effective size unless β is very large ($\sim 10^3$ or higher; Figure 3).
- N_e/N in captivity is unlikely to be larger than about 0.1 (and might be much smaller), so very large values of β are only possible if wild N_e/N is tiny.
- Therefore, a large wild populations undergoing captive enhancement at even modest levels (x about 0.1 or higher) will suffer a major reduction in effective size unless its N_e is a tiny fraction of the census size (α_W about 10^{-4} or lower).
- Programs that are effective in ensuring that overall N_e remains above a specified level can nevertheless cause a large reduction in N_e(treatment) compared with N_e(control) (e.g., all parameter combinations that satisfy $N_e(\text{treatment}) = 500$ in Figure 3 lead to sharp reductions in overall N_e). Even if an effective size of about 500–1,000 is sufficient to provide for most medium-term evolutionary processes, the total number of alleles that can be maintained in a population with effective size of 10^6 is vastly larger than the number that can be maintained in a population with $N_e \sim 10^3$. Ryman et al. (1995b) were probably the first to point out that orders of magnitude reductions in huge fish populations could have a substantial effect on allelic diversity, even if effective population size and heterozygosity remain relatively high. Waples and Naish (2009) discussed this issue and provided a hypothetical numerical example.

The R-L effect presents a conundrum for stock enhancement programs for large marine populations. For such programs, the captive breeders will generally represent a tiny fraction of the wild population (e.g., $N_C/N_W \sim 10^{-4}$ or lower). The general objective of an enhancement program is to take advantage of high survival of early life stages in captivity to boost overall production and/or population size. However, if progeny of captively reared individuals make anything more than a token contribution to the next generation (i.e., x greater than a few percentage), overall N_e will be sharply reduced, unless wild N_e/N is orders of magnitude smaller than captive N_e/N ($\beta \sim 10^3$–10^4 or higher). This implies that any successful marine enhancement program will probably have a severe R-L effect unless the wild N_e/N ratio is about 10^{-4} or smaller. Although tiny genetically based N_e/N estimates this small or smaller have been reported (reviewed by Hedgecock and Pudovkin 2011), such estimates are subject to a variety of potential downward biases and remain controversial (Waples, forthcoming). Furthermore, even if one can confidently conclude that β is quite large, results can be very sensitive to its exact value (Figure 3). Therefore, it is risky to conduct a program whose success depends heavily on difficult-to-evaluate assumptions about the wild N_e/N ratio.

One possible way around this conundrum is to have a very productive enhancement program but harvest most of the captive offspring before they can reproduce in the wild. To what extent this might be feasible is likely to vary considerably by species and locality.

Extreme R-L effects, which can occur with large marine populations, do not require unusual assumptions about reproductive success of captive individuals (e.g., large reductions in overall N_e can easily occur when captive N_e/N is in a "normal" range of 0.1–0.5). However, these extreme R-L effects do require very high captive productivity and very low wild N_e/N. The most plausible explanation for tiny N_e/N ratios in marine species is Hedgecock's (1994) hypothesis of sweepstakes reproductive success, which can be modeled using a multiple-merger coalescent process (Eldon and Wakeley 2009; Eldon et al., forthcoming). The R-L effect in large marine species could produce a similar phenomenon, if a substantial fraction of individuals in the progeny generation can be traced to the relatively few parents used for captive rearing.

Consequences for aquaculture

Marine aquaculture is growing rapidly, and as programs for new species are developed based on capture of wild individuals, the cultured populations might (for a short period, at least) be similar enough genetically to the wild population that the R-L effect is directly relevant. In those situations, the formulas developed here are directly applicable and the issues are similar to those discussed above for marine stock enhancement.

However, commercial aquaculture operations face stiff international competition, and this creates pressure for domesticated populations that have features such as high growth rates, disease resistance, and tolerance of crowding (Gjedrem and Robinson 2014). As noted above, under these conditions, fitness losses that result from interbreeding of wild and domesticated individuals are probably a more serious concern than reduction of effective size due to the R-L effect. A review of genetic risks associated with marine aquaculture can be found in Waples et al. (2012).

Recommendations

We have the following recommendations for scientists, managers, and conservation practitioners. First, it is important that the potential for a Ryman–Laikre effect be taken into consideration in any program for marine stock enhancement and aquaculture. The data necessary to evaluate the effect can be estimated in any captive–wild system by combining methods for estimating census and effective population size with methods for identifying captive offspring in the wild.

Our second recommendation is to establish a consistent, rigorous monitoring program that follows the captive and wild populations over time. Important metrics to monitor include the magnitude and frequency of escapes from closed aquaculture, the frequency of reproductive encounters between captive and wild individuals, the occurrence of F_1 hybrid offspring and backcross descendants in the wild (indicative of genetic introgression), phenotypic variation in key life history traits (e.g., size, age, growth) for both groups, and estimates of within-population genetic diversity as well as wild fitness and productivity (Kapuscinski et al. 2007; Senanan et al. 2007). Ideally, the monitoring programs would be designed so that they can track genetic introgression into wild populations (Karlsson et al. 2014) and ecological/life-history changes in the wild population following introgression (Ford 2002; Reed et al. 2015).

Finally, in addition to methods that can limit the contribution of captively reared offspring to natural spawning, culturists can limit the erosion of N_e in propagation programs by focusing on practices involved in captive breeding that influence $N_{e(T)}$ and β. To minimize inbreeding problems in captivity, captive breeding should strive to maximize diversity among breeders and minimize the variance in adult family size by—to the extent feasible—equalizing breeder sex

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ratios and employing factorial mating schemes that maximize representation of all potential breeders. Such practices have been widely recommended in the fish culture literature.

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Supplementary Material

Supplementary material can be found at http://www.cz.oxfordjournals.org/.

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