An analytical investigation of the dynamics of inbreeding in multi-generation supportive breeding

Pierre Duchesne & Louis Bernatchez*
Département de Biologie, Pavillon Vachon, Université Laval, Sainte-Foy, QC, G1K 7P4, Canada
(**author for correspondence, e-mail: Louis.Bernatchez@bio.ulaval.ca*)

Abstract

Supportive breeding is being increasingly used as a measure to reduce the short-term probability of extinction of populations with highly reduced abundance relative to historical levels. In this paper, we provide a conceptual framework and analytical tools to compute changes in inbreeding coefficient (F) in the case of supportive breeding over any number of generations. The dynamics of inbreeding coefficients were investigated by means of a system of recurrence equations. We focussed on quantifying the dynamics of F for specific combinations of parameter values in terms of the effects of captive population census size, refreshment rate of breeders in captivity, scale of supplementation program, and migration rate. We observed that supplementation did not always result in substantial inbreeding increment and several conditions lowered overall inbreeding relative to control situations without supplementation. The census size of captive populations was the single most important controllable parameter determining the genetic consequences of supportive breeding. While the proportion of captive breeders brought into captivity from the wild bore a complex relationship to inbreeding coefficient dynamics, the results indicated that managers should generally aim at high refreshment rates (that is, large proportions of their captive stock originating from the wild). This is especially important when a small captive population is expected to contribute large numbers of breeders to the supplemented population. The analysis also showed how supplemented populations connected to a large metapopulation through gene flow recover from the genetic risks of inbreeding due to supportive breeding program more quickly than isolated populations. The results of this study join those of an increasing number of investigations showing that supportive breeding does not always increase inbreeding, and may even decrease it in several circumstances. However, supportive breeding systems are complex, and results such as presented here should not be used in isolation, but in consideration of other issues such as the consequences on long-term fitness of wild individuals.

Introduction

Supportive breeding is being increasingly used as a measure to reduce the probability of extinction of populations with highly reduced abundance relative to historical levels (Ryman et al. 1995). This supplementation method is also routinely used in fisheries management in order to sustain exploitation (Waples and Do 1994). Typically, supportive breeding implies that potential parents are caught in a wild population and brought into captivity (e.g. fish hatchery) to increase reproductive and reduce mortality rates,

respectively. Following breeding, some or all of the offspring are returned to the same wild population. This cycle may be repeated over several generations. Supportive breeding may therefore potentially raise the census size of wild populations while circumventing genetic risks associated with admixture of genetically distinct populations, such as outbreeding depression (Utter 1998; Gharrett et al. 1999; Marshall and Spalton 2000).

Highly skewed family size between wild and captive breeders may, however, result in an increased rate of inbreeding as measured by inbreeding coef-

ficients F (Crow and Kimura 1970). Inbreeding effective size N_{eI} was first used by Ryman and Laikre (1991) to measure the effect on F of a single event of supplementation from supportive breeding. This analysis showed that any gain in census size had to be traded against reduction in effective size, but did not account for the fact that census size increments at a given generation increase effective sizes at the next generation. Later, Ryman (1994) and Ryman et al. (1995, 1999) circumvented this problem by substituting the variance effective number (N_{eV}, Crow and Kimura 1970) for N_{eI}. The computation of N_{eV} expressly involves the size of the next, post reproduction, generation and, consequently, N_{eV} changes appear one generation ahead of changes in N_{eI} (Crow and Kimura 1970). Until very recently, the impact of supportive breeding had been evaluated analytically only for a single supplementation. However, the inbreeding effect of multiple generations of supplementation was explored by simulations for the case of Pacific salmonids, *Oncorhynchus* spp. (Waples and Do 1994).

In this paper, we provide a conceptual framework and analytical tools to compute changes of inbreeding coefficient F in the case of supportive breeding over any number of generations. To achieve this, we consider supportive breeding programs as transient systems of two populations, captive and wild, linked together by migration. The inbreeding dynamics within such systems are modelled mathematically as recurrence equation systems. We primarily focus on comparing the dynamics of F under various supportive breeding procedures, given stable, declining and expanding demographic scenarios that comprise pre-supplementation, supplementation and post-supplementation components. The main parameters considered are captive population census size, refreshment rate of breeders in captivity, scale of supplementation program, and migration rate. As such, this study complements in several ways other recent efforts to appraise the genetic consequences of supportive breeding over multiple generations. Namely, Lynch and O'Hely (2001) developed a theoretical framework for assessing the impact of program design on genetic fitness (supplementation load) of natural populations. Wang and Ryman (2001) also used recurrence equations to assess the consequences of multiple generations of supportive breeding on the rates of inbreeding and genetic drift. However, that study primarily focussed on exploring the consequences of different models for selecting

captive breeders as well as that of variance in family size, and did not systematically investigate various demographic scenarios of supplemented populations.

As Waples and Do (1994), we favored F curves (change in inbreeding as a function of time and demographic parameters) as the primary basis for assessing the genetic risks of inbreeding associated with supportive breeding. Translating the dynamics of F into inbreeding effective population size estimates (N_{eI}) may be convenient to describe the overall capacity of a population to resist changes in genetic diversity (Crow and Denniston 1988). However, supportive breeding systems are by definition in a transient state and do not have stable but rather fluctuating effective sizes, which have no more descriptive power than the sequence of F values from which they are derived. Supplementation over many generations raises the question of the proportion of breeders used for supportive breeding that come from the natural population *(W)* relative to the captive population *(H)* (Utter 1998). In the absence of contribution from the natural population, it is quite obvious that inbreeding within such a captive population will rise more rapidly than if it is "refreshed" through the regular input of natural breeders. It is therefore important that F modeling incorporates a *refreshment rate* parameter. Conversely, the proportion among all breeders of *W* of those born in *H* at the previous generation and subsequently contributed to *W* is also an important model parameter (e.g. Ryman and Laikre 1991) that we refer to as the *contribution rate*. A convenient way to account for both refreshment and contribution rates is to view these parameters as migration rates between the captive and wild populations. In this way, supportive breeding may be modeled as a drift-migration process.

Given this conceptual framework, we first developed a *basic model* in which we considered Wright-Fisher ideal random mating conditions for a monoecious diploid species with discrete generations (Hartl and Clark 1997). Since supplemented populations may not be completely isolated from others, we also defined a *metapopulation model* in which gene flow is occurring between the supplemented populations and a much larger group of unsupplemented populations. The dynamics of inbreeding coefficients were investigated by iterating systems of recurrence equations by means of the symbolic calculator Maple®6 (Monagan et al. 2000).

Using these equation systems, we quantified the dynamics of F under several supportive breeding

procedures, given specific demographic scenarios. It is obviously not possible to present a detailed investigation of all possible combinations of parameter values in a single study. Consequently, results were analysed primarily for specific combinations of parameter values in terms of the effects of captive population census size, refreshment rate, scale of program parameters, and migration rate on inbreeding coefficients in wild populations. A detailed investigation of the effects of sex-ratios and variance in reproductive success within the captive and wild populations would justify an elaborate analytical treatment by itself, and consequently will be treated elsewhere.

Methods

Basic model

We consider a migratory system involving one captive *(H)* and one wild *(W)* population. Reproduction is monoecious diploid with selfing. Except for exchange of breeders between *H* and *W*, we assume a Wright-Fisher mating system; that is, reproductive success among breeders is binomial and generations are discrete. The contribution parameter C(k) represents the proportion among all wild breeders in generation k that were born in *H* in the previous generation k – 1. The refreshment parameter R(k) is the proportion among all breeders of population *H* in generation k that were born in *W* in the previous generation k – 1. Both *H* And *W* components reproduce from a mixed stock of breeders (Figure 1). The census sizes of *H* and *W* are noted $N_H(k)$ and $N_W(k)$. Note that R and C respectively correspond to $(1 - r_c)$ and $(1 - r_w)$, where r_c and r_w are the retention parameters recently defined by Lynch and O'Hely (2001) in their study of the impact of supportive breeding on genetic fitness of natural populations.

Recurrence equations

Our purpose is to compute F(k) values. F(k) is defined as the probability that two alleles randomly chosen at generation k are identical by descent. The latter definition allows for consideration of pairs containing one allele from the wild and one allele from captivity. Hence, it is a slight generalization of Caballero's definition (1994) which only considers gametes which can unite to form a zygote. Resolving $F_W(k)$, the probability of identity by descent within the wild population at time k, necessitates the computation

of both $F_H(k)$, the probability of identity by descent within the hatchery population at time k, and $F_{HW}(k)$, the probability of identity by descent of one allele from *H* and one from *W* at time k. This leads to the following system of recurrence equations whose derivation is detailed in the Appendix;

$$F_H(k) = (1 - R)^2 WF(H) + 2(1 - R) \quad (1)$$
$$RF_{HW}(k - 1) + R^2 WF(W)$$
$$F_{HW}(k) = (1 - R)CWF(H) + (1 - R)$$
$$(1 - C)F_{HW}(k - 1) +$$
$$RCF_{HW}(k - 1) + R(1 - C)WF(W)$$
$$F_W(k) = C^2 WF(H) + 2C(1 - C)F_{HW}(k-1)$$
$$+ (1 - C)^2 WF(W)$$

where $WF(X) = 1/(2N_X(k - 1)) + (1 - 1/(2N_X(k - 1)))F_X(k - 1)$ for $X = H, W$

For the sake of simplicity the parameters C and R are represented without (k) generation indexes.

The WF symbol represents a function that produces the expression for the next generation value of F within an ideal Wright-Fisher population (Hartl and Clark 1997). This re-coding function was programmed in the mathematics computer language Maple®6. The use of symbolic processing may allow a substantial reduction in writing as well as conceptual complexity.

Metapopulation model

The above *basic model*, as in all previous investigations of supportive breeding (Ryman et al. 1991, 1995; Waples and Do 1994; Hedrick and Hedgecock 1994; Hedrick et al. 2000; Wang and Ryman 2001), treated wild populations as if completely isolated. Clearly, however, supplemented populations may frequently be linked to unsupplemented ones by gene flow, which will affect the dynamics of F resulting from supportive breeding programs. As a first investigation of the possible effect of gene flow from other populations, we consider the simple and idealized case of a wild population *W* which is a component of a much larger metapopulation *L*. *L* contributes a proportion m of migrants among those breeders of *W* which did not originate from the captive population *H*. Hence, at each generation, the overall proportion of *L* breeders within *W* is (1 – C) M. For simplicity, we assume that an allele brought from the metapopulation at a given generation can never be identical by descent to any allele found in the allelic stock of *W* in the same or any
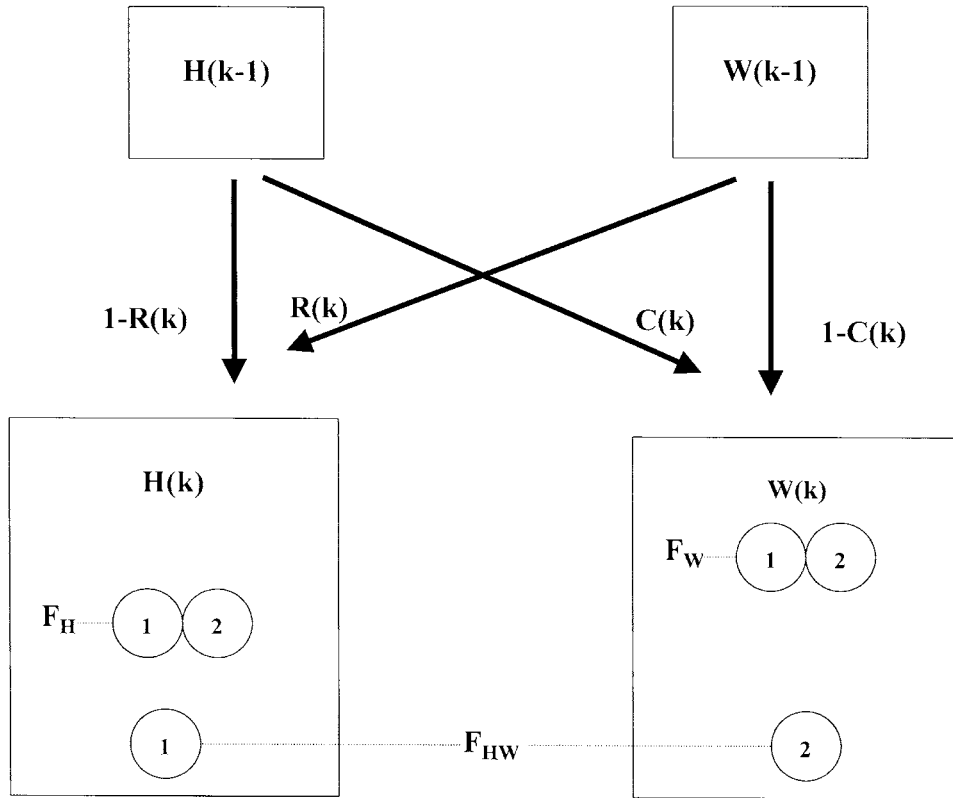
Figure 1. Schematic representation of supplementation at generation k. $H(k-1)$ is the captive population at generation $k-1$. $W(k-1)$ is the wild population at generation $k-1$. The contribution rate, $C(k)$, represents the proportion among all breeders of $W(k)$ of those born in $H(k-1)$ and subsequently contributed to $W(k)$. The refreshment rate, $R(k)$, is the proportion among all breeders of population $H(k)$ of those born in $W(k-1)$ and subsequently contributed to $H(k)$. Circles denote gametes taken at random. F_H, F_W, F_{HW}, refer to captive, wild and captive-wild probabilities of identity by descent.

previous generations. Save gene flow from metapopulation L, all other conditions pertaining to the *basic model* also apply to the *metapopulation model*.

Recurrence equations

Under the *metapopulation model*, the probability that an allele picked at random in $W(k)$ originates from $W(k-1)$ is $(1-C)(1-M)$. In the *basic model* this probability is $(1-C)$. Substituting $(1-C)(1-M)$ for $(1-C)$ in the basic recurrence equations system, we obtain:

$$F_H(k) = (1-R)^2 WF(H) + 2(1-R) \quad (2)$$
$$RF_{HW}(k-1) + R^2 WF(W)$$
$$F_{HW}(k) = (1-R)CWF(H) + (1-R)$$
$$(1-C)(1-M)F_{HW}(k-1) +$$
$$RCF_{HW}(k-1) + R(1-C)$$
$$(1-M)WF(W)$$

$$F_W(k) = C^2 WF(H) + 2C(1-C)(1-M)$$
$$F_{HW}(k-1) + [(1-C)(1-M)]^2$$
$$WF(W)$$

$$\text{Again, } WF(X) = 1/(2N_X(k-1)) + (1-1/$$
$$(2N_X(k-1)))F_X(k-1)$$
$$\text{for } X = H, W$$

Numerical examples of various demographic scenarios

In order to illustrate the usefulness of the above equation systems to depict general trends in the effects of supporting breeding procedures on F, the demographic scenarios of supplemented populations were arranged into three components; pre-supplementation, supplementation and post-supplementation dynamics, respectively lasting two, five and three generations.

Pre-supplementation

We consider *declining*, *constant* and *growing* wild population census sizes. The declining populations start at 200 individuals and undergo a decrease of 10 individuals per generation. The constant populations are composed of 200 individuals in all generations. The census size of growing populations is 200 at k = 0 and increases by 10 at each generation. Linear time functions were chosen for declining and growing sizes mainly for the sake of conceptual simplicity.

Supplementation

We distinguish between *successful* and *unsuccessful* supplementation programs. Although this is certainly not the only measure of success, we define the latter as an increase in the census size of the wild population (N_w) due to the supplementation program. When supplementation is successful, N_w grows by S individuals at each generation; thus, successive sizes are P + S, P + 2S, P + 3S … where S refers to the scale of the supplementation program parameter and P is the last census size of the pre-supplementation period. The successive values of C(k) (contribution parameter) are: S/(P + S), S/(P + 2S), S/(P + 3S), … When supplementation fails, the population keeps its pre-supplementation demographic dynamics. In all scenarios, N_H individuals are lost from the natural population *(W)* to the captive *(H)* at the end of the pre-supplementation period. Hence, the last pre-supplementation size of *W* is less than expected, given its pre-supplementation demography. The census size of the captive population (N_H) is kept constant over all supplementation generations.

Post-supplementation

Successful supplementation may be followed by a crash or a sustained increase (e.g. Waples and Do 1994). In the crash scenario, as soon as supplementation is ended, populations take on the size they would have reached in the absence of supplementation. If sustained increase is achieved, the size is kept constant at the level attained at the end of the supplementation period. Thus, the crash and increase scenarios mean the same as in Waples and Do (1994). Unsuccessful supplementation does not modify the pre-supplementation demography of the population.

Complete scenarios

The impact of supportive breeding on F was explored within the nine complete demographic scenarios resulting from the pairing (cartesian product) of the above components: (declining, constant, growing) X (crash, increase, unsuccessful) (Figure 2). The inbreeding dynamics of any given supplementation program were compared to that of an unsupplemented population (control) with demography identical to the pre-supplementation demography of the compared supplemented populations.

Results

Basic model

Unless otherwise specified, F stands for the inbreeding coefficient of the wild population (F_W) in the remaining text and in figures. For simplicity of presentation, we first analyzed at length the dynamics of F when successful supplementation is followed by a sudden return to pre-supplementation levels as soon as supplementation is halted. Although crash entails previous supplementation success, we refer to the latter scenario as the constant/successful/crash scenario for consistency in scenario nomenclature. Results for the constant/successful/crash scenario are shown graphically in the form of $F_R(k)$ curves (F as a function of k with label R), given a specific pair (N_H, S) of parameter values (Figure 3). In turn, we examined the effects of variable R, S, N_H values, the interactions between S and N_H, as well as the program duration over the dynamics of the inbreeding coefficient F.

R (refreshment rate)

In all four combinations of parameters (N_H, S), the F curves are largest when R = 0; that is, when captive individuals are bred entirely from the previous captive generation. The effect of R on F is decreasing as R increases. For instance, there is a greater leap in F values between R = 0 and R = 0.25 than there is between R = 0.75 and R = 1. Refreshment rate has a much greater impact over time when captive census size N_H is small. Therefore, maintaining a completely genetically isolated captive population appears risky from an inbreeding viewpoint in most situations, and especially so with lower values of N_H. On the other hand, increasing refreshment rates to very high values (0.75–1.0) did not always translate into a substantial reduction of F relative to moderate levels (e.g. 0.25–0.50), especially when N_H was high.
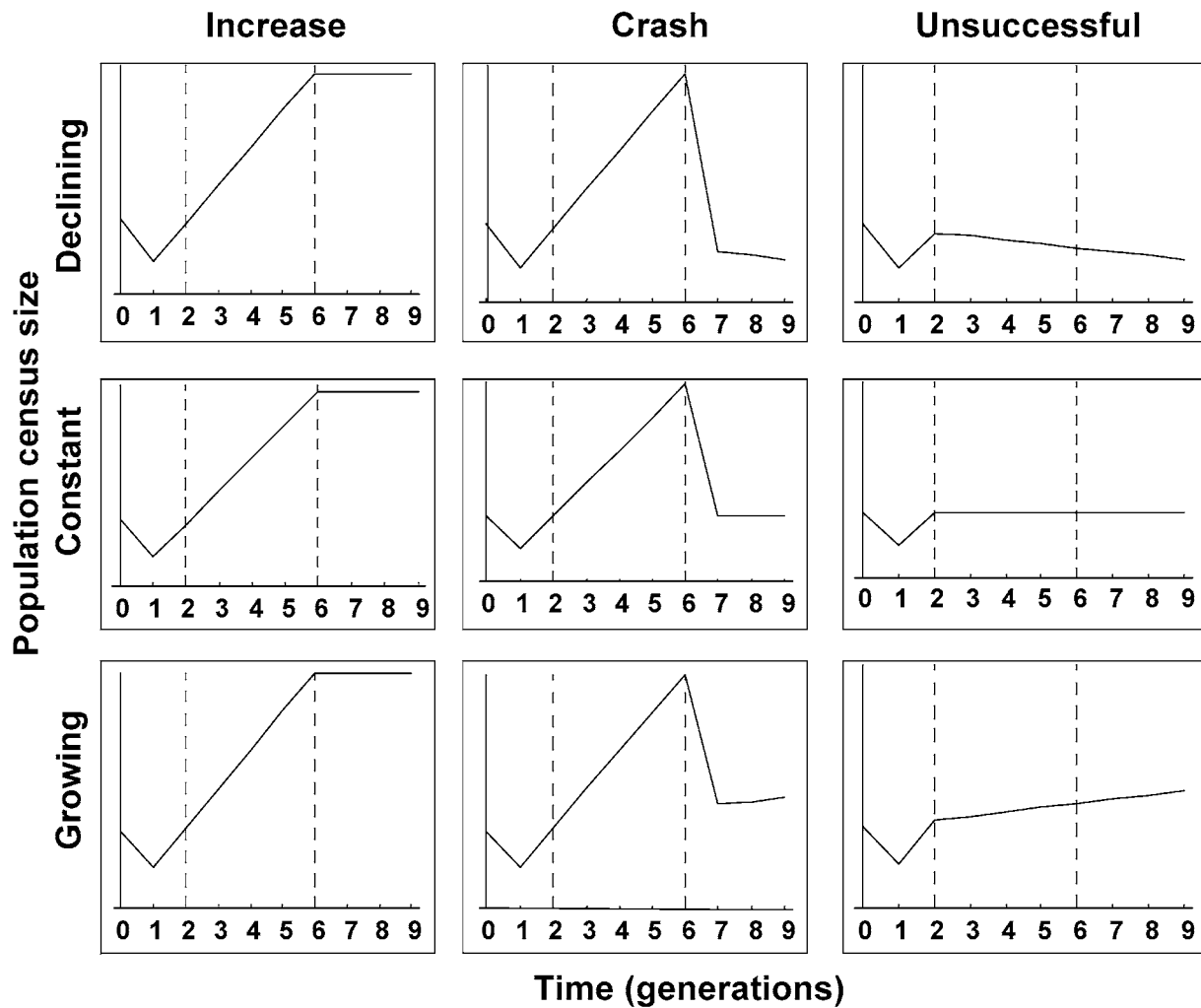
Figure 2. Graphical representation of nine categories of demographic scenarios. From left to right: increase, crash, unsuccessful. From top to bottom: declining, constant, growing. Supplementation periods are bounded by vertical dashed lines. Details are provided in the main text.

S (scale of program)

Given a fixed captive census size N_H, S has a spreading effect over R values; that is, the range of $F_R(k)$ curves increases with S (Figure 3). This means that maintaining a high refreshment rate is particularly beneficial when supplementation is intensive. Also, the spike in F values which takes place on the first generation of supplementation is larger with the larger S. In fact, single generation supplementation with large scales of program show a large spike in F values immediately followed by a leveling out which lasts a single generation (not shown). However, this leveling out effect will not generally compensate for the large initial inbreeding increase. Hence single generation supplementation programs are more detri-

mental when the scales of supplementation program are large, which is entirely consistent with previous findings of Ryman and Laikre (1991), Waples and Do (1994), Ryman et al. (1995). The above relationships were found consistently over all scenarios (data not shown).

N_H (census size of captive population)

Given a fixed scale of supplementation program S, N_H has two main effects over F (Figure 3). First, $F_R(k)$ curves for smaller captive populations are higher for all R values. For example, when $N_H = 10$ (S = 100), all $F_R(k)$ curves stand above the control curve (no supplementation) whereas they all stand below
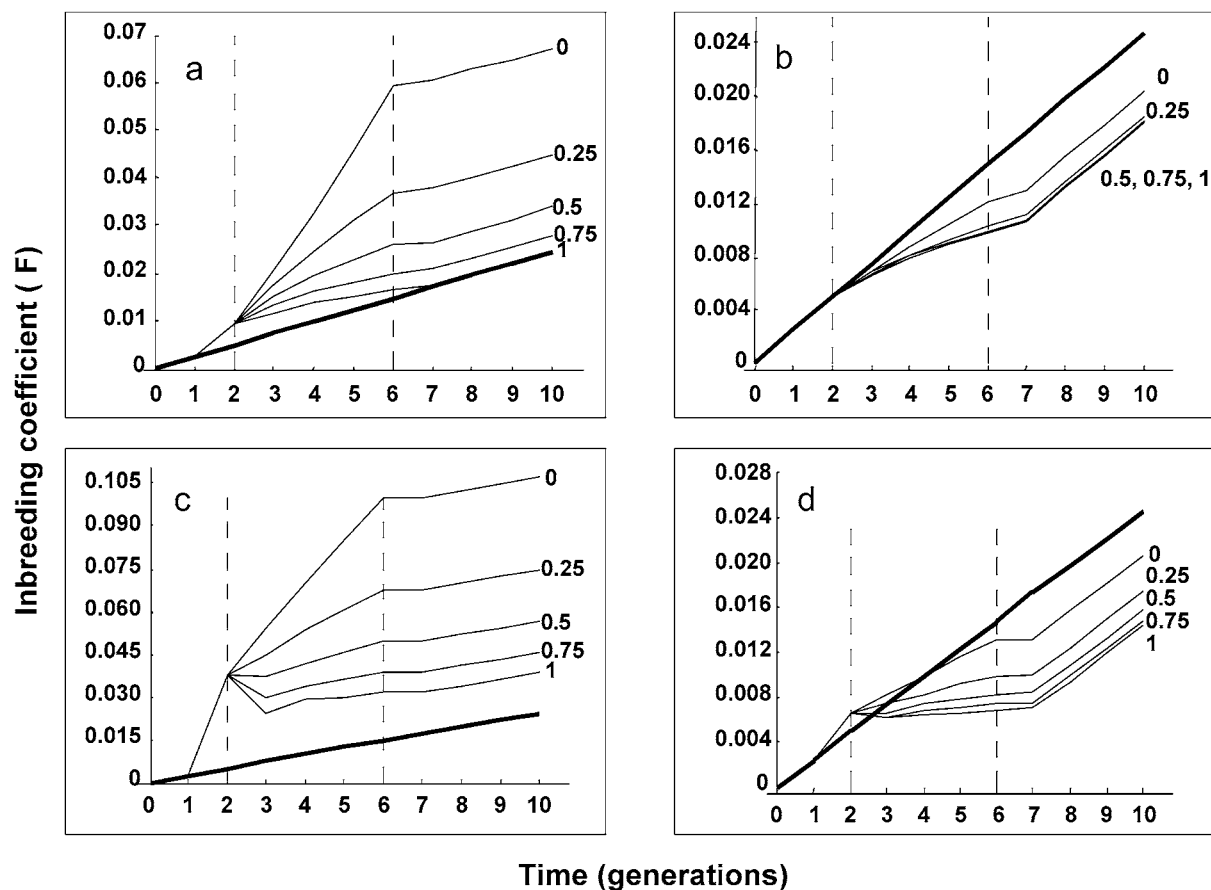
Figure 3. Influence of captive census size N_H, scale of program S and refreshment rate R within a constant/successful/crash scenario. Curves are tagged according to R: a, N_H = 10 and S = 100; b, N_H = 100 and S = 100; c, N_H = 10 and S = 1000; d, N_H = 100 and S = 1000. Supplementation periods are bounded by vertical dashed lines. In each panel, solid dark line is the control (no supplementation).

the control when N_H = 100 (S = 100). Second, in contrast to S, N_H has a compressing effect over R, in that it reduces the distances between F_R(k) curves. Hence refreshment rate values are of a lesser concern with larger captive populations. These two trends were observed over all scenarios and all parameter (N_H, S) combinations (data not shown).

S (scale of program) and N_H (captive census size) interactions

Apart from its effects over height of spike and spread of F curves over R values, S values did not reveal a regular scaling effect over F. Thus, increasing S may either decrease or increase F, depending on the captive population census size N_H. For instance, when N_H = 10, raising S from 100 to 1000 results in an overall increase in F, whereas when N_H = 100, it produces a general decrease of F (Figure 3). More

generally, given a specific supplementation generation k, with increasing S, F(S) shows either a rapid increase (N_H = 10) or decrease (N_H = 100) followed by a much slower approach towards an R dependent asymptotic value (Figure 4). Hence, increasing scale values of the supplementation program will not necessarily bring any sizeable increase of F, all other parameters being equal.

Program duration

Although not considered explicitly a parameter in this study, the number of generations of supplementation may determine the outcome of F relative to the control level (no supplementation). For instance, with parameter values N_H = 100, S = 1000, R = 0, five generations of supplementation result in a reduction of F, while a two-generation program would lead to a net increase (Figure 3d). This indicates that all else
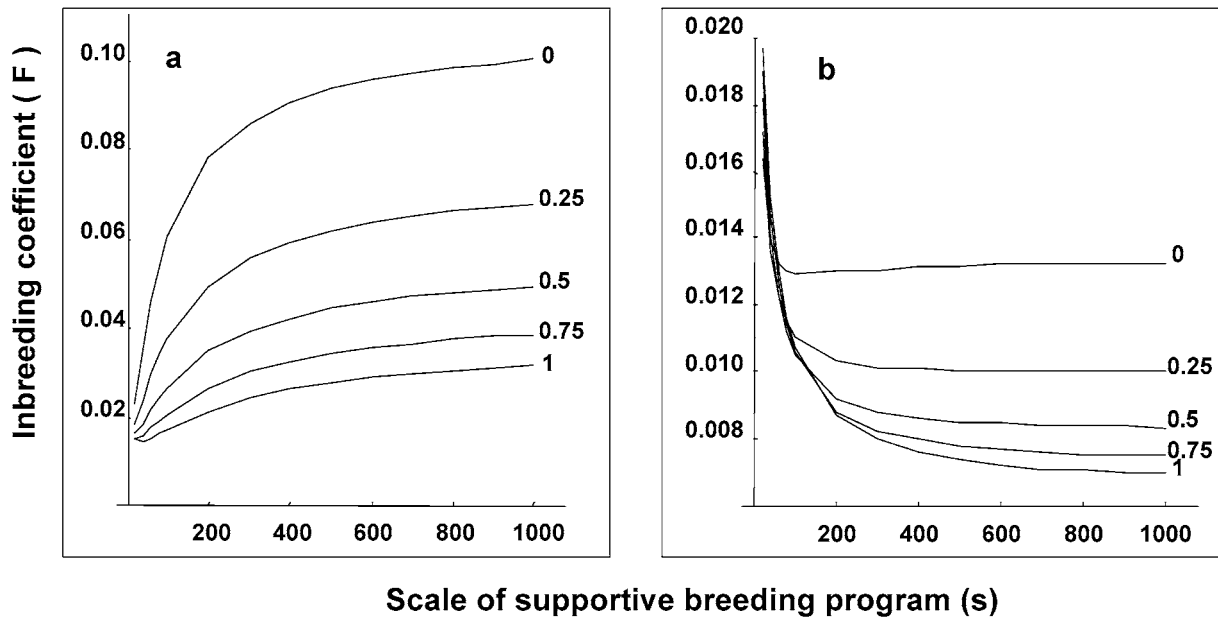
Figure 4. Comparison of the influence of scale of program S between: a, low ($N_H = 10$) and b, high captive census size ($N_H = 100$). F is evaluated one generation after the end of the supplementation period. Curves are tagged according to refreshment rate R. Demographic scenario is constant/successful/crash.

being equal, the effect of program duration over F should also be taken into account when planning a supplementation program (see also Waples and Do 1994).

Constant/unsuccessful scenario

Most observations pertaining to the constant/successful/crash scenario apply as well to the constant/unsuccessful scenario (Figure 5). Basically, F values are higher than in the constant/successful/crash scenario. However, these differences are much larger in the case of the smaller captive size, which again points to the prevailing effect of this parameter. Consequently, supplementing from a relatively large captive population should be considered to reduce the risks of inbreeding associated with unsuccessful supplementation.

Declining, constant and growing scenarios

Among the nine demographic scenarios (Figure 2), only with unsuccessful supplementation did we find substantial differences among scenarios with declining, constant and growing pre-supplementation components (not shown). Therefore, we focus the subsequent analysis on unsuccessful supplementation scenarios. With all four combinations of (N_H, S) parameter values, F curves take on their largest values with

the declining scenario, while the smallest values of F were obtained with the growing scenario. However, when F curves are compared to their respective controls, declining populations are overall closer to the control situation than are constant or growing populations. These trends are illustrated in Figure 6 in the case of $N_H = 100$ and S = 1000. One main observation from these comparisons is that unsuccessful supportive breeding programs may most often result in increased inbreeding of wild populations unless refreshment rates are maintained high, e.g. above 0.5.

Crash vs increase successful scenarios

The differences between crash and increase post-supplementation scenarios are readily predictable from theory (Hartl and Clark 1997). A sudden return to pre-supplementation demography (crash) produces rates of increase of F which are identical to those found in the control F at each post-supplementation generation save the first one (Figure 3). Thus, under crash scenarios, the level of F at the end of the supplementation period appears critical, since it may determine a durable increase or decrease in F as compared to no supplementation. In the case of sustained population increase, rates of increase of F will be lower than control over subsequent generations (not shown).
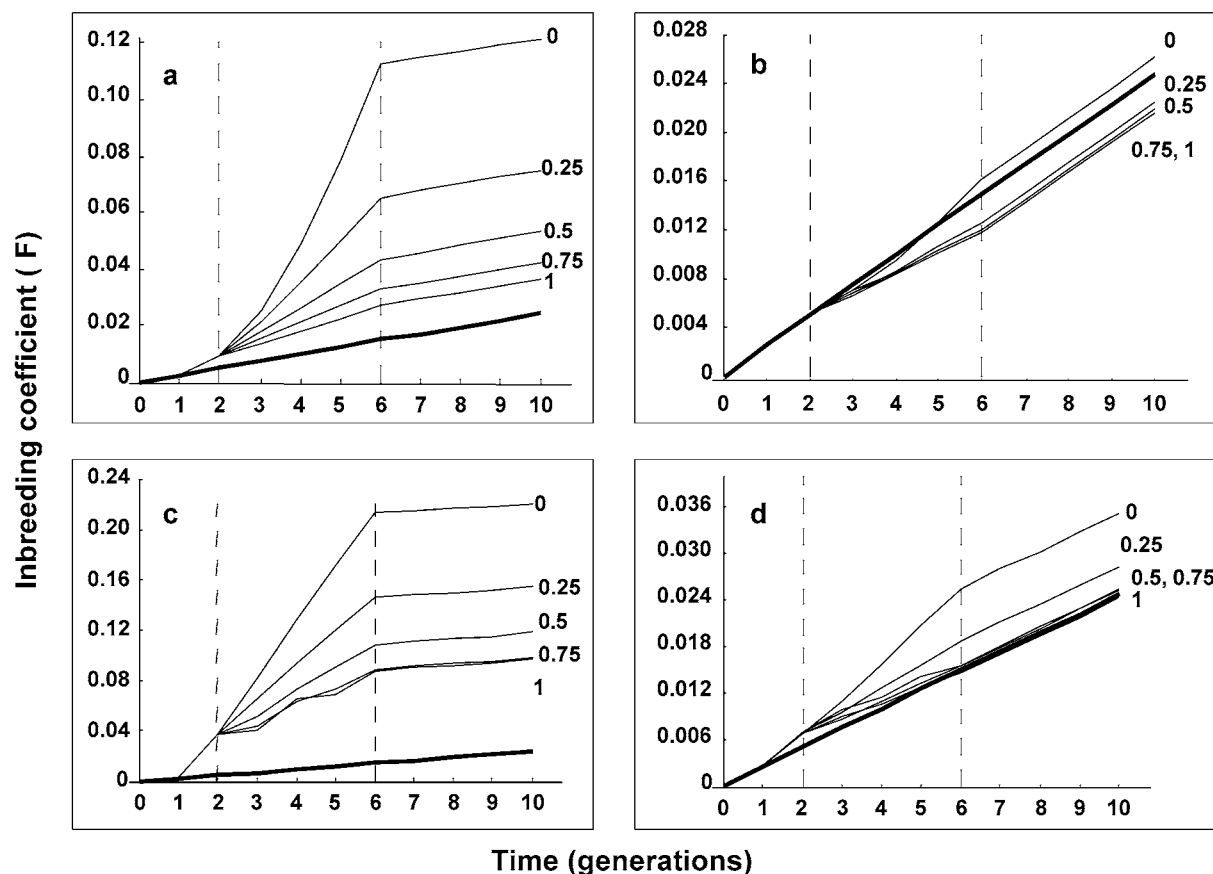
Figure 5. Influence of captive population census size N_H, scale of program S and refreshment rate R within a constant/unsuccessful scenario. Curves are tagged according to R: a, $N_H = 10$ and S = 100; b, $N_H = 100$ and S = 100; c, $N_H = 10$ and S = 1000; d, $N_H = 100$ and S = 1000. Supplementation periods are bounded by vertical dashed lines. In each panel, solid dark line is the control (no supplementation).

Metapopulation model

In the *metapopulation* model, the wild Population W is considered a subpopulation of a much larger breeding unit L. We first considered the effect of the migration parameter M over generations within the constant/successful/crash scenario, and then examined its interactions with the refreshment rate R and the size of captive population N_H.

The analyses were restricted to parameter values $N_H = 10$ and S = 1000 (Figure 7). Higher values of M are associated with lower F curves for all refreshment rate values and these differences increase over supplementation generations. In the post-supplementation period, given a fixed M > 0, all $F_R(k)$ curves converge to the same M-dependent equilibrium value, say f_M, the larger M values being associated with smaller values of f_M (Hartl and Clark 1997). Moreover, systems with larger migration rates have higher rates

of convergence. This means that M has a buffering effect over the rise of inbreeding coefficient due to supplementation. That is, wild populations connected to a large metapopulation through substantial gene flow will tend to recover from the genetic risks of inbreeding due to supportive breeding program more quickly than isolated populations.

Discussion

The main objective of this paper was to provide a conceptual framework and analytical tools to handle the computation of F in the case of supportive breeding over any number of generations. To achieve this, we considered supportive breeding programs as transient systems of two populations, captive and wild, linked together by migration. The inbreeding dynamics within such systems were modeled mathematically
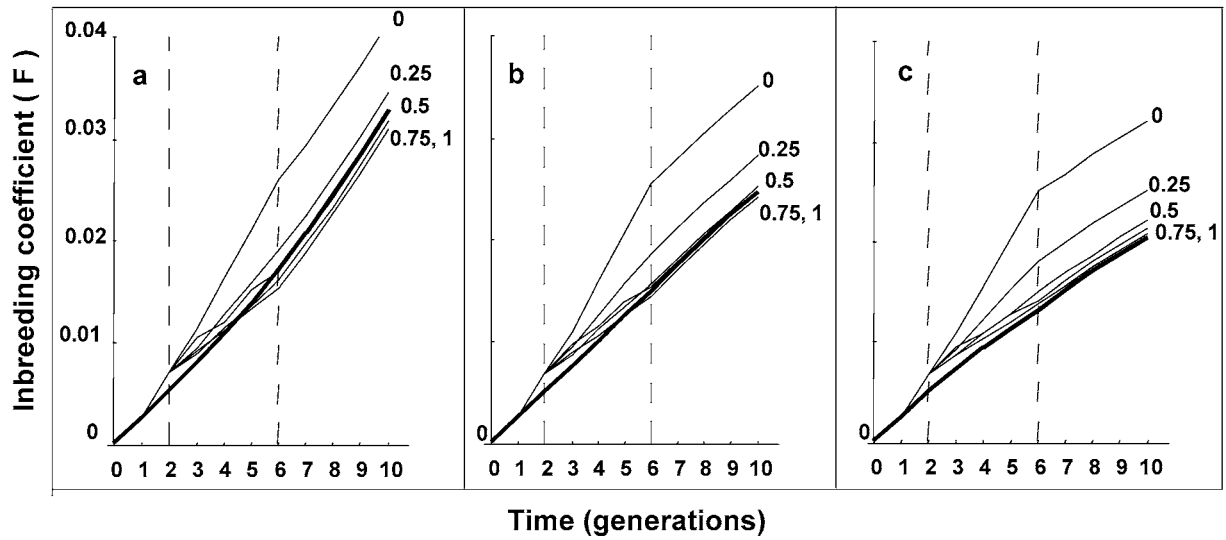
Figure 6. Influence of pre-supplementation demographies when supplementation is unsuccessful: a, declining; b, constant; c, growing scenarios. In all three graphs captive census size N_H = 10 and scale of program S = 1000. Supplementation periods are bounded by vertical dashed lines. In each panel, solid dark line is the control (no supplementation).
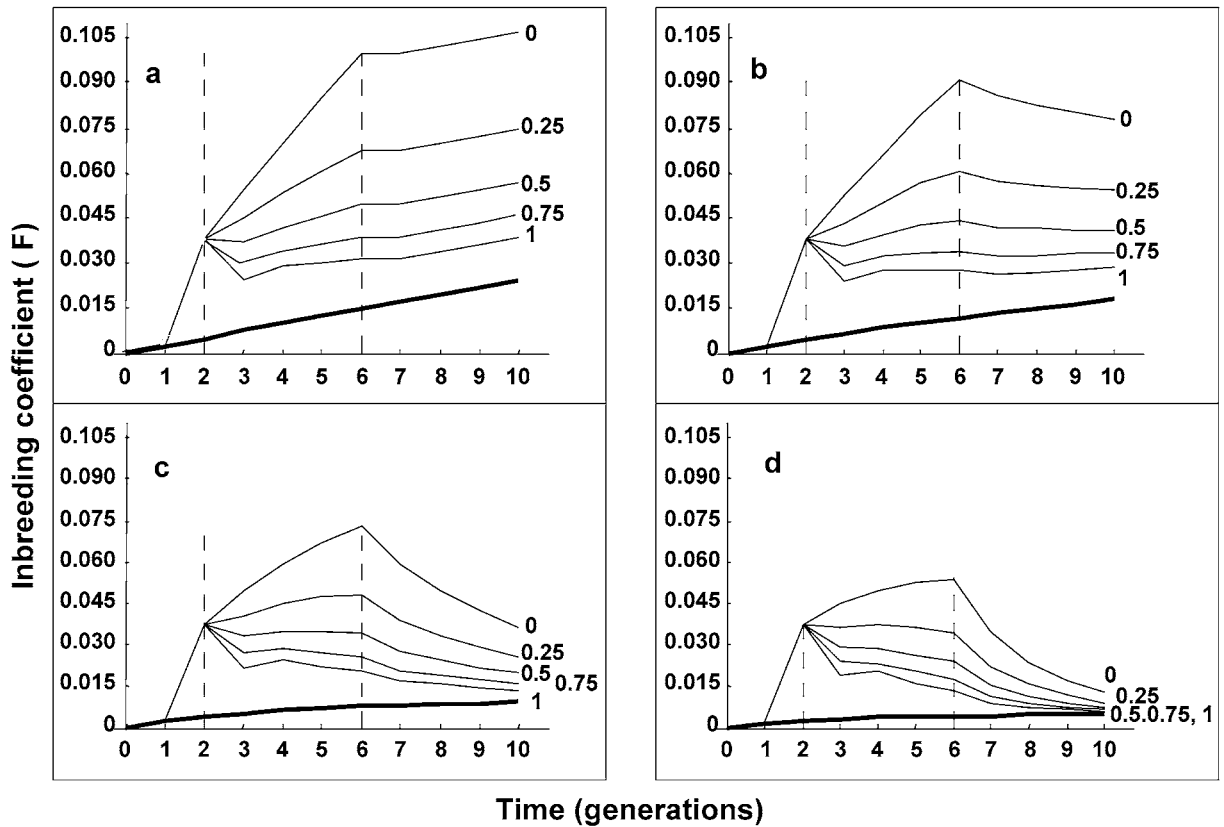

Figure 7. Influence of the migration rate M over pre-supplementation, supplementation and post-supplementation generations. Values of M are: a, 0; b, 0.05; c, 0.1; d, 0.2. In all four graphs captive population census size N_H = 10 and scale of program S = 1000. Curves are tagged according to refreshment rate R. Demographic scenario is constant/successful/crash. Supplementation periods are bounded by vertical dashed lines. In each panel, solid dark line is the control (no supplementation).

as recurrence equation systems. These were used to compare the dynamics of F under various supportive breeding procedures, given specific demographic scenarios that comprised pre-supplementation, supplementation proper and post-supplementation components. In the following discussion we assume that both captive and wild populations satisfy the Wright-Fisher model and as a consequence have equal effective and census sizes. While the main qualitative conclusions can be generalized to populations with effective sizes different from census sizes, Ne/N ratio would of course have to be considered for designing supportive breeding programs of "real" populations departing from the Wright-Fisher model (see below).

In principle, the complex dynamics of F within multi-generation supportive breeding programs may be tackled either through simulations (e.g. Waples and Do 1994) or recurrence equations systems as used here. Since it produces near exact solutions in virtually no time, the latter technique allows for fast and extensive exploration of mathematical relationships, compared to simulations. Conversely, recurrence equations systems may potentially be of such complexity as to make them extremely difficult to develop. However, this need not be the case since symbolic complexity can be handled by using symbolic calculators.

Globally, our findings were in agreement with Waples' (1999) contention that there is no valid general statement as to the consequences on genetic diversity of supportive breeding procedures over multiple generations. The dynamics of F within the context of supplementation is a complex function of several potentially manageable parameters such as the census size of captive populations, refreshment rates, the scale of supplementation program and its duration. F is also subjected to largely uncontrollable conditions, such as gene flow from other wild populations, as well as variable demographic conditions during the period of supplementation and afterwards. As previously reported by Waples and Do (1994) (see also Cuenco 1994), and more recently by Wang and Ryman (2001), we found that under many conditions, supplementation did not result in substantial inbreeding increment relative to control situations. In fact, several conditions lowered overall inbreeding relative to control situations without supplementation. For instance, given a constant/successful/crash scenario with $N_H = 100$, $S = 1000$, all refreshment values produced F values below control at the end of the five generation supplementation program. Even

with unsuccessful supplementation that does not result in any increase of census size, an inbreeding reduction was observed under some parameter combinations. For instance, given a constant/unsuccessful scenario with $N_H = 100$, $S = 100$, all refreshment rates equal to or over 0.25 produced F values below control for the entire supplementation period. This phenomenon may potentially be attributed to a transitory population subdivision effect. Wang and Caballero (1999) have shown that under some, but not all, migration regimes, metapopulations with constant overall census size have higher effective sizes than a single population of the same census size.

The census size of the captive population was found to be the single most important controllable parameter determining the effect of supportive breeding on genetic risks of inbreeding. This was revealed by the simulation study of Waples and Do (1994) within the specific context of captive broodstock programs of Pacific salmonids. Although our objective was not to investigate in details the relationship between inbreeding dynamics and captive census size, we generally observed that increasing N_H was always beneficial in terms of inbreeding reduction, and especially so with small captive population size. The influence of the scale of supplementation program S was also highly dependent upon census size of the captive population. Given low values of the latter, increasing the scale was detrimental as it quickly raised F levels. Given higher values of N_H, however, increasing the scale resulted in a fast reduction of F. In both cases F(S) curves quickly converged to an asymptotic value. This suggests that given a sufficiently large captive census size relative to census size of wild populations, intensive supplementation programs may theoretically be run without too much concern over inbreeding increment under some circumstances. The practical problem is of course to determine such a critical census size for the captive population. A possible practical solution could be to bring into captivity as many breeders as possible. This, however, may be associated with important drawbacks, such as increased risks of directional genetic changes, risks to the remaining natural population through mining wild broodstock, and risks of catastrophic failure of captive populations (discussed in Waples and Do 1994). Consequently, future efforts should be devoted to find practical means of assessing critical captive census sizes in the form of approximation formulae. Monitoring changes in genetic diversity in the wild population as well as differential mortality rate and

reproductive success of individuals of captive and wild origin would also be most useful in that perspective.

The proportions of captive breeders brought into captivity from the wild (refreshment rate R) also bore a complex relationship to inbreeding coefficient dynamics. However, under all conditions considered, F was more responsive to R with smaller captive population census sizes and larger scales of supportive breeding. In addition, curves representing no refreshment (totally genetically isolated captive population) always had higher values, most often standing far apart from other F curves. Clearly, one should generally aim at high refreshment rates in supportive breeding, especially so when a small captive population is expected to contribute large numbers of breeders to the supplemented population.

The supplemented population may be part of a large metapopulation that provides it with a proportion of migrants at every generation. During the supplementation period, such systems always had lower inbreeding coefficients than did ones without migration. Furthermore, this differential effect increased with each additional supplementation generation. As expected, inbreeding coefficients were found to decrease with increasing migration rate. In the post-supplementation generations, rises in F due to supplementation eventually vanished in populations that were part of a metapopulation, and the pace of this cleansing effect was faster with higher values of M. These observations indicate that supplementation risk assessment should take into account the level of gene flow between supplemented and neighboring populations. They also suggest that assuming complete genetic isolation of supplemented populations may in some circumstances potentially lead to overly conservative predictions regarding rates of inbreeding.

We also found that failure of supportive breeding to increase census size was less detrimental (relative to respective unsupplemented control situations) to declining populations than to either constant or growing populations. This trend was also most noticeable when refreshment rates were low. In the case of successful programs, the increase versus crash scenarios showed dramatic and readily predictable post-supplementation differences. As increase scenarios may generally be too optimistic (Waples and Do 1994), crash scenarios following supplementation should be considered as a more conservative outcome since a rise in inbreeding at the end of supplementation (relative to unsupplemented demographies) could cause long term genetic risks of inbreeding.

Limitations of this study

This study dealt primarily with reproduction processes satisfying most of the Wright-Fisher model assumptions. Real reproductive systems involve many deviations from this simplifying model, such as biased sex ratios, non-random variance in family size and overlapping breeding generations. In order to solve these complex systems, we plan to make extensive use of symbolic processing. The effects over F of several additional parameters will have to be explored and analyzed systematically, which was beyond the scope of the present study.

This study provided insights into the mathematical nature of the general relationships between inbreeding coefficient and several demographic parameters. In a next step, the effect of these parameters on F could be modeled more accurately, at least under some standard reference conditions. As previously presented by Ryman and Laikre (1991) for a single supplementation event, a systematic investigation of captive population census size as a parameter controlling the impact of scale of program over inbreeding dynamics will be of particular interest. Also, demographic declines and expansions were all assumed to be linear, whereas real demographic dynamics may generally involve more complex, density-dependent recruitment functions, and have consequences on temporal changes in inbreeding (Waples and Do 1994). The impact of demography should therefore be further assessed by running extensive computations under different demographic models.

The metapopulation model indicated that the occurrence of gene flow between supplemented and non-supplemented populations may have major impacts on the dynamics of inbreeding in supportive breeding. Strictly speaking, however, this model is only valid for situations where supplemented populations are embedded in a much larger metapopulation. Therefore, conclusions pertaining to the metapopulation model should not readily be extended *a priori* to more complex systems, for instance where the supplemented population is linked by gene flow to one or few populations of variable and roughly similar finite sizes. It therefore remains to investigate the inbreeding effect of supplementation in the context of collections of sub-populations under a variety of migration models.

To conclude, the results of this study join those of an increasing number of investigations showing that supportive breeding may, in some circumstances, reduce inbreeding rates relative to unsupplemented

populations (Cuenco 1994; Waples and Do 1994; Ryman et al. 1995; Wang and Ryman 2001). As pointed out by Waples and Do (1994), however, captive broodstock programs have a very complex nature, and results such as those we presented here should not be used in isolation, but in consideration of all other possible consequences of such programs (e.g. Utter 1998; Waples 1999). For instance, Lynch and O'Hely (2001) theoretically showed that maximizing effective population size (either inbreeding or variance) may not necessarily minimize the genetic supplementation load in all circumstances.

Acknowledgements

Appendix: Derivation of recurrence equations for basic model

We consider a migratory system involving one captive *(H)* and one wild *(W)* population. Reproduction is monoecious diploid with selfing. Except for exchange of breeders between *H* and *W*, we assume a Wright-Fisher mating system; reproductive success among breeders is binomial and generations are discrete. The proportion of breeders contributed by *H* to *W* at generation k is C(k) and that of breeders contributed by *W* to *H* is R(k). Hence each of *H* and *W* reproduce out of a mixed stock of breeders (Figure 1). The sizes of *H* and *W* at generation k are noted $N_H(k)$ and $N_W(k)$. Our purpose is to compute F values, i.e. probabilities that two alleles, say A1 and A2, picked at random at generation k, are identical by descent. Let F_W, F_H, and F_{HW} denote F values when A1 and A2 are randomly chosen in *W*, *H*, and in both *H* and *W*, one in *H* and the other in *W*, respectively. Although we are mainly concerned with $F_W(k)$, we have to simultaneously compute $F_H(k)$ and $F_{HW}(k)$.

Basic events and associated F values

When, at generation k, one picks alleles A1 and A2 at random, four events may take place:

hh: A1 came from *H(k – 1)*, A2 came from *H(k – 1)*
hw: A1 came from *H(k – 1)*, A2 came from *W(k – 1)*
wh: A1 came from *W(k – 1)*, A2 came from *H(k – 1)*
ww: A1 came from *W(k – 1)*, A2 came from *W(k – 1)*

To each of these events there corresponds a specific F value:

	F
Hh	$1/(2\,N_H(k-1)) + (1 - 1/(2\,N_H(k-1)))\,F_H(k-1)$
Hw	$F_{HW}(k-1)$
Wh	$F_{HW}(k-1)$
Ww	$1/(2\,N_W(k-1)) + (1 - 1/(2\,N_W(k-1)))\,F_W(k-1)$

Note that events **hh** and **ww** are products of Wright-Fisher mating processes taking place at generation k – 1, hence their associated F value at generation k (Hartl and Clark 1997).

Recurrence equations as weighted sums

To compute $F_H(k)$, we need to weigh the above F values against the probabilities of occurrence of the four events (**hh, hw, wh, ww**), given that A1 and A2 are both picked in *H*(k). Writing R instead of R(k), these probabilities are respectively: $(1 - R)^2$, $(1 - R)\,R$, $R\,(1 - R)$, R^2.

Then $F_H(k)$ is equal to the weighted sum of all four possible events:

$$F_H(k) = (1 - R)^2 WF(H) + 2(1 - R)R F_{HW}(k - 1) + R^2 WF(W)$$

where for any Wright-Fisher population *X*:

$$WF(X) = 1/(2N_X(k - 1)) + (1 - 1/(2N_X(k - 1)))F_X(k - 1)$$

Reasoning along the same lines, we obtain recurrence equations for $F_W(k)$ and $F_{HW}(k)$. Together the equations for $F_H(k)$, $F_W(k)$ and $F_{HW}(k)$ make up the system of recurrence equations shown in the *Basic model* section. This system was cast into matrix form to iterate and produce sequences of numerical probability by descent vectors $\mathbf{F(k)} = (F_H(k), F_{HW}(k), F_W(k))$.

References

Caballero A (1994) Developments in the prediction of effective population size. *Heredity*, **73**, 657–679.

Cuenco, ML (1994) A model of an Internally Supplemented Population. *Trans. Am. Fish. Soc.*, **123**, 277–288.

Crow JF., Kimura M (1970) *An Introduction to Population Genetics Theory*. Burgess, Minneapolis.

Crow JF, Denniston C (1988) Inbreeding and variance effective population numbers. *Evolution*, **42**, 482–495.

Denniston C (1978) Small population size and genetic diversity. In: *Endangered Birds: Management Techniques for Preserving Endangered Species* (ed. Temple SA), pp. 281–302. University of Wisconsin Press, Madison.

Gharrett AJ, Smoker WW, Reisenbichler RR, Taylor SG (1999) Outbreeding depression in hybrids between odd- and even-broodyear pink salmon. *Aquaculture*, **173**, 117–129.

Hartl DL, Clark AG (1997) *Principles of Population Genetics*, 3rd edition. Sinauer Associates, Sunderland, Massachusetts.

Hedrick PW, Hedgecock D (1994) Effective population size in winter-run chinook salmon. *Cons. Biol.*, **8**, 890–892.

Hedrick P, Hedgecock D, Hamelberg S, Croci S (2000) The impact of supplementation in winter-run chinook salmon on effective population size. *J. Hered.*, **91**, 112–116.

Lynch M, O'Hely M (2001) Captive breeding and the genetic fitness of natural populations. *Cons. Gen.* (in press).

Marshall T, Spalton J (2000) Simultaneous inbreeding and outbreeding depression in reintroduced Arabian oryx. *An. Con.*, **3**, 241–248.

Monagan MB, Geddes KO, Heal KM, Labahn G, Vorkoetter SM, McCarron J (2000) *Maple 6 Programming Guide*. Waterloo Maple, Inc., Waterloo, Canada.

Ryman N (1994) Supportive breeding and effective population size: differences between inbreeding and variance effective numbers. *Cons. Biol.*, **8**, 888–890.

Ryman N, Laikre L (1991) Effects of supportive breeding on the genetically effective population size. *Cons. Biol.*, **5**, 325–329.

Ryman N, Jorde PE, Laikre L (1995) Supportive breeding and variance effective population size. *Cons. Biol.*, **9**, 1619–1628.

Ryman N, Jorde PE, Laikre L (1999) Supportive breeding and inbreeding effective number: reply to Nomura. *Cons. Biol.*, **13**, 673–676.

Utter, F (1998) Genetic problems of hatchery-reared progeny released into the wild, and how to deal with them. *Bull. Mar. Sc.*, **62**, 623–640.

Wang, J, Ryman N (2001) Genetic effects of multiple generations of supportive breeding. *Cons. Biol.* (in press).

Waples, RS (1999) Dispelling some myths about hatcheries. *Fisheries*, **24**, 12–21.

Waples RS, Do C (1994) Genetic risk associated with supplementation of Pacific salmonids: captive broodstock programs. *Can. J. Fish. Aquat Sc.*, **51** (Suppl. 1), 310–329.

Wang J, Caballero A (1999) Developments in predicting the effective size of subdivided populations. *Heredity*, **82**, 212–226.

Wright, S (1931) Evolution in Mendelian populations. *Genetics*, **16**, 97–159.