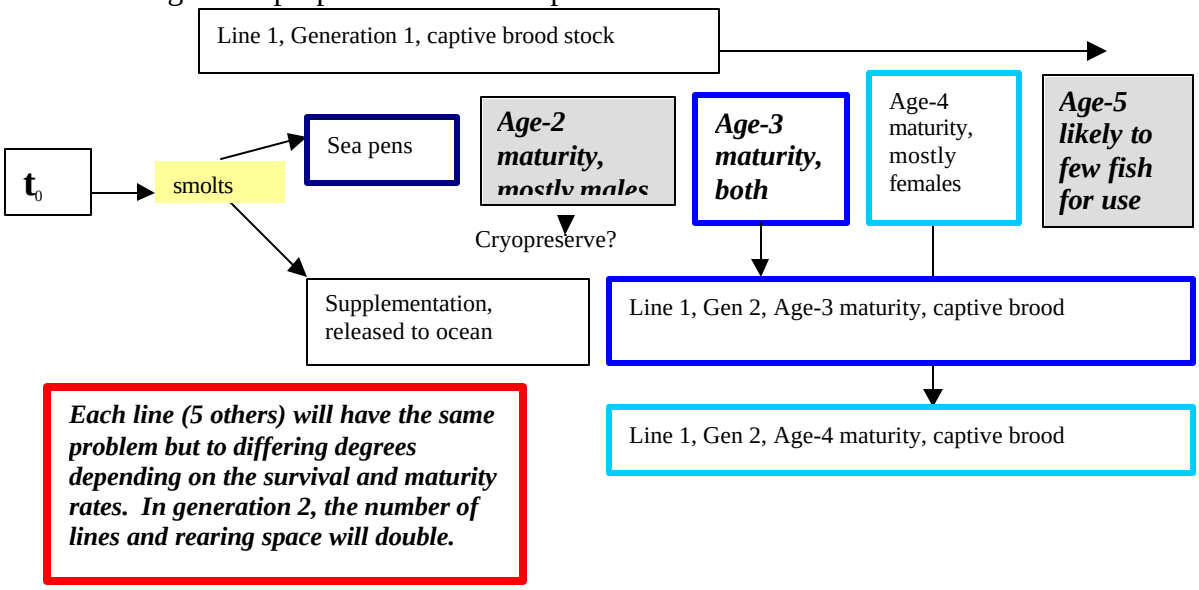
ProjectID: 35037

Measuring the potential for domestication selection of spawn timing in chinook captive and supplementation programs; implications for recovery.
Sponsor: UW and NMFS
FY03 Request: $129,498
5YR Estimate: $718,893
Short Description: Analyze the genetic response to (and recovery from) inadvertent domestication selection for spawn timing in supplementation and captive programs, using quantitative genetic approaches to trend analysis
Response Needed? Yes

ISRP Preliminary Comments:
The development of a quantitative genetic program in Pacific salmon is a welcomed addition, and we encourage the proponents to continue to develop their experimental design. We are uncertain about some aspects of the proposed research and are concerned about others:

ISRP: The experiment would be initiated in one spawning year and the second generation selected within lines and age-class. However, in the F2, generation selection at age-3 and then age-4 will generate two separate lines; this generates a risk of causing a bottleneck within the original selection lines (-ve, control, +ve lines). Further, unless there was good survival and maturity at ages 3 and 4, to produce sufficient numbers of progeny for the next generation only a very limited selection pressure and differential may be possible. This is a diagram of our understanding of the proposed selection experiment:

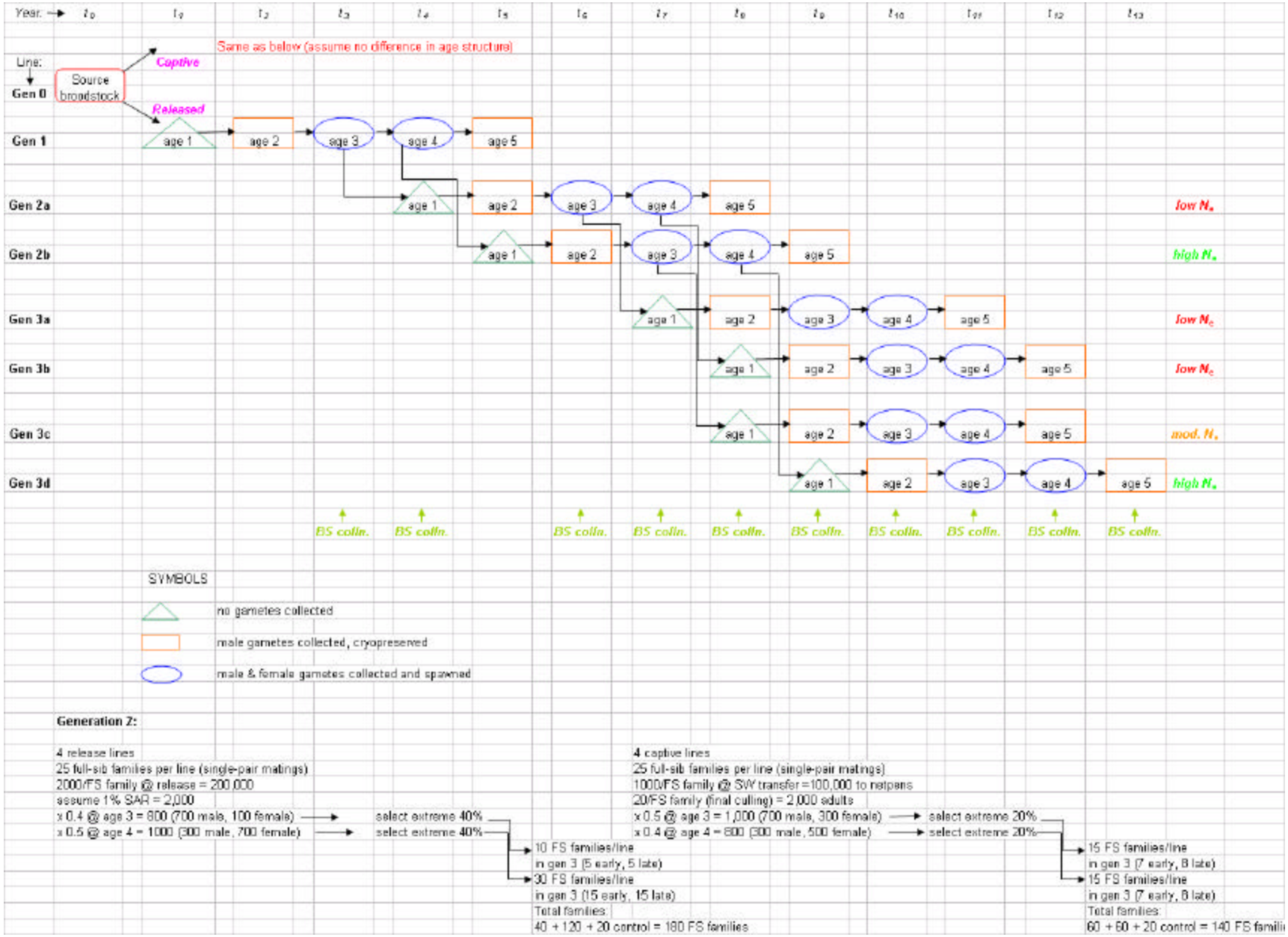


The proponents should clarify how they planned to deal with this scenario or demonstrate how their design would avoid this bottleneck.

Author response: The ISRP has pointed out a number of potential problems that make this sort of experiment very challenging to design, implement, and analyze; we regret not discussing these in sufficient detail initially. We have outlined the design in the following diagram under an option that entails a three-generation divergent selection experiment on chinook salmon for early and late spawning, with a corresponding unselected control line, and under a scenario in which the initial broodstock is collected in a single year. The bottleneck referred to above cannot be avoided, but we do not think this problem prevents analysis of selection response or outweighs the advantage of chinook salmon as an experimental animal to investigate hatchery domestication. In preparing this proposal, we discussed at length the possibility of using coho salmon for this study but elected to involve chinook salmon for several reasons that are outlined in the last comment to the ISRP, found below.

The design involves divergent selection with an unselected control under two regimes: hatchery release, and captively reared. The inclusion of both "regime" groups is critical to the study for two reasons: it allows greater flexibility in how selection is implemented within a cohort (with perhaps double the selection intensity possible in a captive vs a released population), and it allows evaluation of response to selection in two different environments. Briefly, to address the bottleneck problem, we would maintain and monitor separate experimental lines that differ in their effective size, and analyze the observed selection responses for genetic contribution using approaches that account for variation in genetic drift and sample size (Falconer 1954, Hill 1972, Hard et al. 1993, Lynch and Walsh 1998). We would then evaluate the variation in direct and correlated response to selection using a partial regression approach that treats the unselected control line as a covariate to adjust estimates of response for effects of within-generation line x environment interaction (Muir 1986, Hard 1991).

The experiment, if carried through three generations, would as the ISRP noted become quite large (over 300 full-sib family groups). But the UW facility can accommodate a design this large if long-term freshwater culture is not required (as in fall chinook salmon), and captive marine rearing to adulthood is possible (available at NMFS' Manchester and Mukilteo field stations). We plan to mark family groups (and in some cases individuals) uniquely to combine groups in common garden environments and facilitate breeding.


Year: → t0 t1 t2 t3 t4 t5 t6 t7 t8 t9 t10 t11 t12 t13
Same as below (assume no difference in age structure)
Line:
Gen 0
Source broodstock
Captive
Released
Gen 1
Gen 2a
Gen 2b
Gen 3a
Gen 3b
Gen 3c
Gen 3d
age 1
age 2
age 3
age 4
age 5
low Ne
high Ne
mod. Ne
BS collin.
SYMBOLS
no gametes collected
male gametes collected, cryopreserved
male & female gametes collected and spawned
Generation 2:
4 release lines
25 full-sib families per line (single-pair matings)
2000/FS family @ release = 200,000
assume 1% SAR = 2,000
x 0.4 @ age 3 = 800 (700 male, 100 female)
x 0.5 @ age 4 = 1000 (300 male, 700 female)
select extreme 40%
select extreme 40%
10 FS families/line
in gen 3 (5 early, 5 late)
30 FS families/line
in gen 3 (15 early, 15 late)
Total families:
40 + 120 + 20 control = 180 FS families
4 captive lines
25 full-sib families per line (single-pair matings)
1000/FS family @ SW transfer = 100,000 to netpens
20/FS family (final culling) = 2,000 adults
x 0.5 @ age 3 = 1,000 (700 male, 300 female)
x 0.4 @ age 4 = 800 (300 male, 500 female)
select extreme 20%
select extreme 20%
15 FS families/line
in gen 3 (7 early, 8 late)
15 FS families/line
in gen 3 (7 early, 8 late)
Total families:
60 + 60 + 20 control = 140 FS famili

ISRP: There seem to be three possible approaches:
1) Initiate each line with adequate numbers of families/individuals to minimize this risk (this would be very dependent upon the freshwater facilities available)
Authors: This option is favored by us in an experiment that involves chinook salmon. As noted above by the ISRP, this is a complex experiment that will pose substantial logistical challenges. Nevertheless, we believe it can be accomplished with adequate planning and care. The basic analysis is relatively straightforward; the complications introduced by genetic drift and genotype-environment interaction can be dealt with by incorporating models that account for these confounding effects on evolutionary response.

We favor this option for the study over option #2 because it takes into account age structure, factoring it directly into the analysis, but requires fewer individual groups than option #3.

Freshwater at the UW hatchery is derived mainly from Portage Bay, the adjacent water body. There is no limitation to this water supply or to the means of water delivery. The main constraints for this experiment are the number of available tanks and the availability of cool water for rearing in spring. We have a large space in which to plumb extra tanks, and we will be able to support the numbers of chinook salmon families and individuals we propose in the above diagram.

ISRP: 2) Select only one age-class for selection in the second generation, but this would have a significant effect on the desire to study correlated traits also.
Authors: We do not favor this option for the reason stated by the ISRP. Refer to the diagrammatic description of the proposed experiment (which describes option #1).

ISRP: 3) Initiate the study during 2 or 3 years and determine how to conduct the selection during the second generation. How would a selection differential be determined with over-lapping brood years?
Authors: This option would increase the number of lines required by about two-fold over option #1; therefore, we do not favor it. Refer to the diagrammatic description of the proposed experiment (which describes option #1).

ISRP: Objective 5 indicates that at least 2 generations will be followed and that further generations will be followed. There's no analysis of how much response to selection may be observed in so few generations—there may be little evident response.
Authors: Our estimate of heritability of spawn timing for Puget Sound fall chinook salmon (Grovers' Creek Hatchery population) is 0.24; the estimate of heritability of age at maturity is 0.35, and that for the genetic correlation between these traits is about + 0.07 (Hard, in press). Assuming that we can impose a cumulative selection intensity on spawn timing of 12 phenotypic standard deviations (approximately 15 days between the means of early and late spawners) over three generations, we may expect a cumulative response for spawn timing of at least 3 phenotypic standard deviations over this period, which should be detectable with the proposed approach.

ISRP: The proposal also refers to using DNA analysis to monitor inbreeding in the lines. While it is not stated, we presume that the "pedigrees" refer to will not be used during the selection

process and only used in tracking the change of inbreeding over time. If the potential effect of domestication is to be studied, then pedigrees should not be used to direct any of the matings.
Authors: The presumption made by the ISRP regarding use of pedigree information to guide selection is correct; we do not intend to use pedigree information to direct any matings.

ISRP: Domestication is a real concern in the use of artificial propagation and is deserving of experimental measurement and selection on return timing/spawn timing is known to be a source of domestication selection. While it's understandable to want to observe correlated changes in maturation age in selected chinook, the difficulty of this experiment and the impractically long time commitment required by the experiment suggests that an experiment on a less complex, shorter lived, salmon, e.g. coho, would be more informative and could provide useful results within ten years. Studies of correlated responses could still be conducted on other traits (e.g. size at maturity, growth rate, fecundity). Further, the space required for these species may be more consistent with that available, and if coho salmon were used their survival rate would likely be sufficient to maintain a reasonable selection differential in the selected lines.

Authors: In our discussions that led to the design of this project, we weighed the benefits of using one species over the other. We justified our choice of chinook salmon as a study species for this experiment on grounds of both scientific interest and logistics:

- We believe that age at maturity is an important trait to study in a species with a relatively complex life history as well as those traits identified by the ISRP. For example, if domestication selection inadvertently affects age at maturity, then the gene flow between generations and hence the effective population size will change. Many hatchery salmon populations have shown phenotypic changes in both spawn timing and average age at maturity (as well as other traits) over the span of a few decades. The proposed experiment involving chinook salmon would provide information relevant to potential selection on both of these traits imposed by domestication and by harvest (again, these traits are genetically correlated and important constraints to hatchery broodstock collection; Hard, in press).
- Coho salmon are typically maintained in captivity for a year before release – the power of comparison between the levels of domestication proposed in this experiment would therefore be reduced. The need to culture these fish long-term at times of year when temperatures are high limits our ability to maintain a natural coho salmon life history, and increases the hazard of catastrophic loss during captive culture.
- Chinook salmon is of high priority for recovery planning in the Columbia River Basin, in Puget Sound, and around the Pacific Northwest.
- Survival rates, including marine survival rates, for chinook salmon at the UW hatchery are relatively high (1% SAR to the hatchery broodstock collection facility), and we think adequate for the release component of the proposed selection experiment.
- Coho salmon merit serious consideration for a hatchery domestication selection experiment, but we have had a harder time envisioning a suitable stock and facility for conducting a study involving this species. Pink salmon also have considerable appeal but our access to hatchery pink salmon is highly restricted and their life history much simpler, limiting the range of potential analyses.

Action Agency/NMFS RME Group Comments:

1. Address critical element of RPA?

RME comments: Although this proposal does not directly address either RPA 182 or 184, it may have some relevance to both.

With respect to RPA 184, this proposal relates to hatchery reforms aimed at lessening domestication selection. The comparison of levels of domestication selection between supplementation programs and captive brood programs might provide insight on which types of conservation hatcheries have the potential to contribute to recovery, compared to their respective domestication risks.

Author comment: The experiment provides not only a comparison between hatchery supplementation and captive brood programs, but should also provide information on how quickly selection in a hatchery can produce detectable domestication effects for several key life history traits.

RME comments and opposing view. Of some relevance to RPA 184. Basic research, but not directly linked to what hatchery operators could apply in the real world to reform hatcheries. The problem already is "addressed," albeit imperfectly, by measures designed to minimize domestication selection.

Author comment: Current reforms are based on random mating protocols and maintenance of large effective population sizes. It is not known whether these measures are effective in reducing domestication. It is also not known to what extent stocks with hatchery history can be used for recovery planning. This study has considerable power over current studies examining the reintroduction success of hatchery fish in the wild using kinship studies. Each of these kinship-based studies are case specific and are dependent on variables such as hatchery history, generations under cultivation, the degree of domestication selection within each stock and of numbers of wild fish in the target population. We disagree that the problem is already being addressed to any meaningful extent, and domestication selection is too poorly characterized to guide any measures that might be implemented. Our experiment directly determines *direction* and *magnitude* of domestication selection and highlights the opportunity to counter such selection with broodstock collection (and the costs of doing so). It also examines the correlated response in a number of other traits under selection and provides a broader picture of the effects of domestication on the genetic variability underlying a number of fitness traits within a population.

RME comments: With respect to RPA 182, a study of domestication may provide information on a potential genetic risk of hatchery fish spawning in the wild, i.e. outbreeding depression. Likewise, the inadvertent selection for altered run timing, and the transmission of those traits to wild fish via hatchery fish spawning in the wild, may be a valid biological concern.

Author comment: We agree with this statement.

2. Scope? [ESU's covered, Transferability, Species covered]

RME comments: Puget Sound Chinook ESU. Single species/ESU. Uncertain transferability.

Author comments: Such a study is unlikely to be as successful if it were staged in the Columbia River Basin, because the return rates would not be as high as that experienced at the University of Washington Hatchery. We believe that the findings are highly transferable; as we state above, the information can be used to determine the appropriateness and utility of a specific stock with a history of hatchery domestication for recovery efforts. We should also obtain information on the number of generations that stocks can be cultured under conventional hatchery conditions before maladaptive effects are detected for any of several key life history traits.

3. Study design adequate, as is, or as may be modified? Important basic research. The data from this proposal concerning levels of inbreeding, however, might have limited, i.e. site specific, application, since the experimental populations at the UW have been under culture for several generations.

Author comment: We do not propose to examine inbreeding in this study, although inbreeding rates will be monitored. Under Objective 1, in Part 2 (page 11), we state that we intend to introduce a new wild-type run to the UW hatchery, if possible.

References cited:

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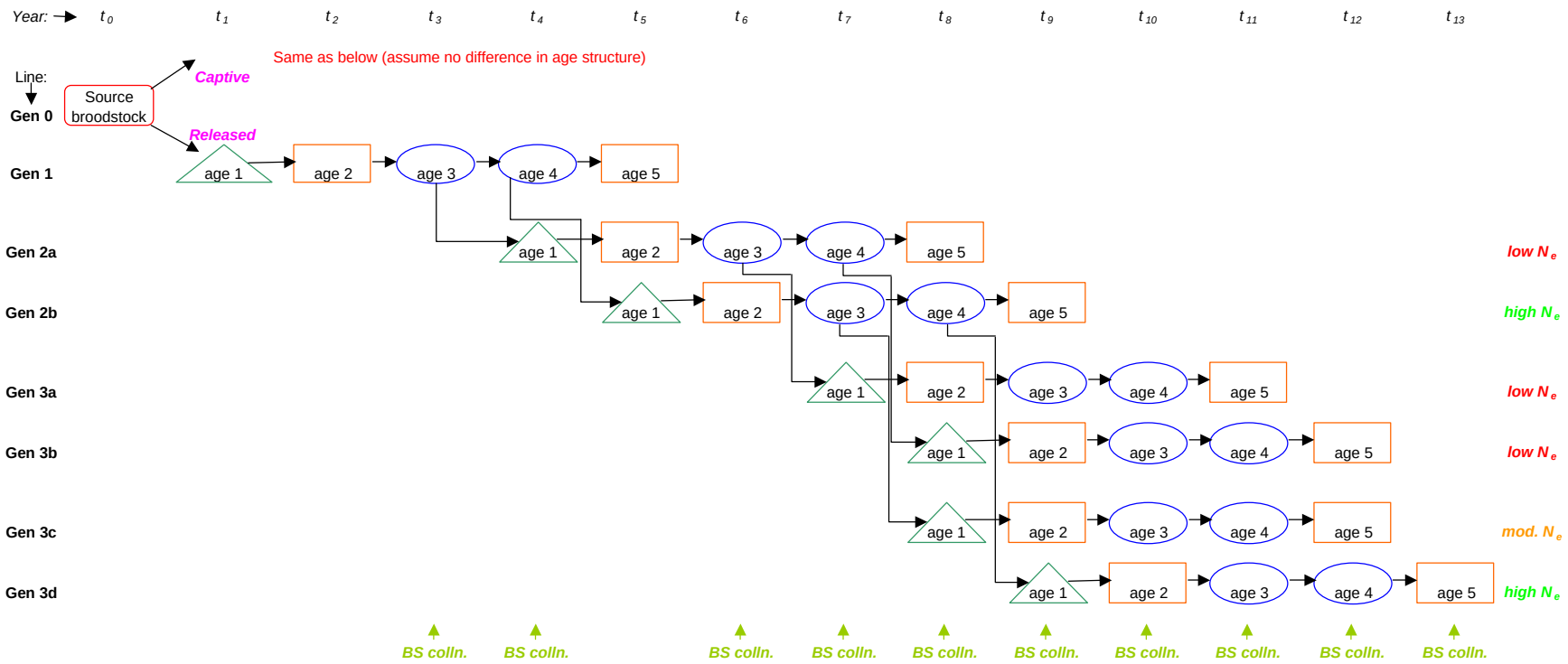
Muir, W. M. 1986. Estimation of response to selection and utilization of control populations for additional information and accuracy. Biometrics 42:381-391.



SYMBOLS

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