Truncation selection for BLUP-EBV and phenotypic values in fish breeding schemes
Anna K. Sonessona,*, Bjarne Gjerdeb, Theo H.E. Meuwissenb

aAKVAFORSK (Institute of Aquaculture Research Ltd), P.O. Box 5010, 1432 Ås, Norway
bInstitute of Animal and Aquacultural Sciences, Agricultural University of Norway, P.O. Box 5003, 1432 Ås, Norway

Received 26 March 2004; received in revised form 23 September 2004; accepted 26 September 2004

Abstract

We have compared rate of inbreeding (ΔF) and genetic gain (ΔG) in truncation selection schemes for fish on best linear unbiased prediction (BLUP) estimated breeding values (EBVs; BTS) or phenotypic values (PTS) with one constraint on the number of tanks (100 or 200) to rear the families, e.g., until tagging size, and one constraint on the total number of selection candidates (3200 or 6400). Single trait selection was practiced for a trait with heritability of 0.1, 0.4 or 0.7 and 5, 10, 20, 50, 100 or 200 selected sires and dams were selected. When going from PTS to BTS, we found an overall increase of ΔG and ΔF of a factor of 0.07 and 1.45, respectively; that is, the increase of ΔG was moderate and accompanied by a dramatic increase of ΔF. In general, ΔF was reduced by increasing the number of tanks at a given number of selection candidates and by decreasing the number of selection candidates at a given number of tanks. ΔF was also reduced for schemes with high heritability because BLUP breeding value estimation then increases the weight on the individual’s phenotype, which leads to a reduced correlation between BLUP estimated breeding values within a family, and fish from more families become selected. In practical fish breeding schemes, PTS seems preferable over BTS because BTS generally give unacceptable high ΔF (≥0.01) for these schemes with few but large families. PTS can, however, only be used for traits measured on the selection candidate, which makes PTS less valuable for schemes with comprehensible breeding goals, including, for example, growth, disease resistance, maturity and fillet quality traits. Several traits are measured today on sibs only.

© 2004 Elsevier B.V. All rights reserved.

Keywords: Fish breeding; BLUP; Truncation selection

1. Introduction

The state of the art method to estimate breeding values is the Best Linear Unbiased Prediction (BLUP; Henderson, 1984) method. BLUP uses information of the candidate (if available) and all
its relatives, which increases the accuracy of these estimated breeding values (EBVs). Truncation selection on BLUP-EBVs is a standard selection method, where individuals with the highest EBVs are selected and get the same number of offspring although modifications might be used in selection schemes in practice. For schemes that select for one trait that is measured on the candidate, truncation selection on phenotypic values (PTS) is a simpler alternative. BLUP truncation selection (BTS) results in higher genetic gain but also higher rate of inbreeding ($\Delta F$) than phenotypic truncation selection (PTS) due to high correlation of estimated breeding values within families, such that the selected animals originate from only a few families (Wray and Thompson, 1990). When comparing the methods at the same $\Delta F$, neither PTS nor BTS has been found generally superior with respect to genetic gain in schemes with different levels of heritability, population sizes, number of selected animals, etc. (e.g., see Quinton et al., 1992; Villanueva and Woolliams, 1997). In general, the methods differently affect accuracy of selection and selection intensity, which in turn both affect the response of selection. Accuracy of selection increases by the use of information on relatives, but it also increases $\Delta F$. Selection intensity increases by selecting fewer animals, which in turn increases $\Delta F$. PTS resulted in higher genetic response than BTS for small schemes (5 sires and 50 dams selected out of 100 candidates; Verrier et al., 1993) and for schemes with $\Delta F$ lower than 0.017 (Quinton et al., 1992). Villanueva and Woolliams (1997) reported that index selection was superior to PTS for large schemes with low heritability of 0.1. With increasing heritability, PTS and BTS become more alike, which is expected, because in BLUP, the weight on the individual’s phenotype increases as heritability increases (Henderson, 1984). The efficiency of PTS and BTS has not been compared for typical fish breeding schemes, in which large family groups can be produced, and schemes that use information on relatives are limited by the number of family groups (i.e., tanks) that can be held separately for the period before tagging. In this paper, we compare the efficiency of truncation selection on phenotypic values and BLUP estimated breeding values (BTS) for typical fish breeding programs. In particular, we will compare genetic gain and rate of inbreeding for schemes with different size (number of selection candidates and selected sires and dams), number of tanks and trait heritability.

2. Methods

The structure of the simulated breeding scheme was that of a closed nucleus with discrete generations. Genetic values were simulated according to the infinitesimal model (Bulmer, 1985). Genotypes, $g_i$, of the unrelated base animals were sampled from the distribution $N(0, \sigma_g^2)$ where $\sigma_g^2$ is the base generation genetic variance, which was 0.1, 0.4 or 0.7. The trait was recorded on an equal number of males and females before selection. Record $y_i$ was calculated as $y_i = g_i + e_i$, where $e_i$ is the environmental effect, which was sampled from $N(0, 1 - \sigma_e^2)$ making the base generation phenotypic variation ($\sigma_p^2$) equal to 1.0. Later generations were obtained by simulating offspring genotypes from $g_i = 0.5g_s + 0.5g_d + m_i$, where $s$ and $d$ denote sire and dam of offspring, respectively, and $m_i$ is the Mendelian sampling component, which was sampled from $N(0, 0.5(1 - F_{sd})\sigma_g^2)$, where $F_{sd}$ is the average inbreeding coefficients of the sire and the dam.

Record $y_i$ was the selection criteria for the PTS schemes. BLUP-EBVs were calculated according to Henderson (1984) and used as selection criteria for the BTS schemes. An overall mean was the only fixed effect, and animal and environmental effects were random. The estimation of BLUP-EBVs also assumes the infinitesimal model; that is, the distributional assumptions made to simulate the data and to analyse the data using BLUP were exactly the same.

Out of 3200 or 6400 selection candidates, 5, 20, 50, 100 or 200 sires and an equal number of dams were selected each generation; that is, the scheme was symmetric with respect to number of selected sires and dams. The selected parents came from 100 or 200 tanks, which often is limiting in practical BTS schemes in fish. The 3200 or 6400 candidates were reared in 100 or 200 rearing tanks. Each tank contained (number of candidates)/(number of tanks) fish, which were produced by one mating between one male and one female. The male and female parent of each tank was sampled with replacement from the
group of selected sires and dams; that is, mating was at random. This random mating design implies that the sizes of the full- and half-sib families varied between replicates, and the results therefore reflect an average over all possible family sizes.

Presented results are the $\Delta F$ and $\Delta G$ of truncation selection on BLUP-EBVs (BTS) and phenotypic values (PTS) at generation 10, when the scheme had reached equilibrium. The average of 25 replicated simulations is presented.

3. Results

Rate of inbreeding ($\Delta F$) and genetic gain ($\Delta G$) are shown in Fig. 1a for schemes with 3200 selection candidates, heritability of 0.1, 0.4 or 0.7 and 5, 20, 50 or 100 selected sires and dams. Because the offspring of 200 sires and dams could not be tested in only 100 tanks, the scheme with 200 selected sires and dams is not included in Fig. 1a. In general, $\Delta F$ of 0.01 or lower are considered acceptable in breeding schemes (e.g., see Goddard, 1992). The $\Delta F$ of the BTS scheme was higher than 0.01 for all three heritability estimates.
and number of selected parents, in particular, for schemes with low heritability of 0.1. For schemes with 100 selected sires and dams, $\Delta F$ of PTS schemes was at or below the acceptable rate of inbreeding of 0.01. The $\Delta G$ was similar for BTS and PTS at the same number of selected sires and dams and generally highest for schemes with 20 and 50 selected sires and dams. For schemes with higher heritability of 0.4 and 0.7, which were schemes where $\Delta G$ of PTS and BTS resembled each other more, $\Delta G$ was somewhat higher for PTS than BTS. As expected, $\Delta G$ was higher for schemes with a high heritability of 0.7 than for schemes with a low heritability of 0.1.

Results in Table 1 show that, for the scheme with 3200 selection candidates, 100 selected parents and heritability of 0.4, the effect of increasing the number of tanks from 100 to 200, gave a statistically significant decrease in $\Delta F$ from 0.026 to 0.017 for BTS and a nonsignificant decrease from 0.008 to 0.006 for PTS. $\Delta G$ was significantly increased from 0.609 $\sigma_p$ to 0.688 $\sigma_p$ for BTS and nonsignificantly reduced from 0.610 $\sigma_p$ to 0.592 $\sigma_p$ for PTS.

The effect of increasing the number of selected parents from 100 to 200 for schemes with 200 tanks, 3200 selection candidates and heritability of 0.4 was a significant decrease of $\Delta F$ from 0.017 to 0.004 for BTS and a significant decrease from 0.006 to 0.004 for PTS. $\Delta G$ was significantly decreasing from 0.717 $\sigma_p$ to 0.624 $\sigma_p$ for BTS and from 0.654 $\sigma_p$ to 0.561 $\sigma_p$ for PTS.

For schemes with heritability of 0.1, similar results were shown except that the standard error was larger here, such that fewer comparisons were significant than for the schemes with heritability of 0.4. For schemes with heritability of 0.7, similar results were shown as for schemes with heritability of 0.4.

For schemes with an increased number of selection candidates from 3200 to 6400 (Tables 1 and 2), the general tendency was that $\Delta F$ did not change, and $\Delta G$ increased.

### Table 1
Rate of inbreeding ($\Delta F$) and genetic gain ($\Delta G$) for schemes with different number of tanks (Ntanks), selection method (Sel method), number of selected parents (Nselected) and heritability levels ($h^2$) for schemes with 3200 selection candidates per generation

<table>
<thead>
<tr>
<th>Ntanks</th>
<th>Sel method*</th>
<th>Nselected</th>
<th>$\Delta F$ (se)</th>
<th>$\Delta G$ (se) ($\sigma_p$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>$h^2=0.1$</td>
<td></td>
</tr>
<tr>
<td>100</td>
<td>BTS</td>
<td>100</td>
<td>0.051 (0.007)</td>
<td>0.231 (0.009)</td>
</tr>
<tr>
<td></td>
<td>PTS</td>
<td>100</td>
<td>0.008 (0.001)</td>
<td>0.178 (0.006)</td>
</tr>
<tr>
<td>200</td>
<td>BTS</td>
<td>100</td>
<td>0.033 (0.004)</td>
<td>0.231 (0.013)</td>
</tr>
<tr>
<td></td>
<td>PTS</td>
<td>200</td>
<td>0.019 (0.001)</td>
<td>0.223 (0.007)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>100</td>
<td>0.005 (0.001)</td>
<td>0.173 (0.005)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>200</td>
<td>0.004 (0.001)</td>
<td>0.149 (0.005)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$h^2=0.4$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>100</td>
<td>BTS</td>
<td>100</td>
<td>0.026 (0.003)</td>
<td>0.609 (0.011)</td>
</tr>
<tr>
<td></td>
<td>PTS</td>
<td>100</td>
<td>0.008 (0.001)</td>
<td>0.610 (0.013)</td>
</tr>
<tr>
<td>200</td>
<td>BTS</td>
<td>100</td>
<td>0.017 (0.002)</td>
<td>0.688 (0.009)</td>
</tr>
<tr>
<td></td>
<td>PTS</td>
<td>200</td>
<td>0.009 (0.001)</td>
<td>0.558 (0.007)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>100</td>
<td>0.006 (0.001)</td>
<td>0.592 (0.010)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>200</td>
<td>0.004 (0.001)</td>
<td>0.525 (0.009)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$h^2=0.7$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>100</td>
<td>BTS</td>
<td>100</td>
<td>0.014 (0.002)</td>
<td>0.982 (0.016)</td>
</tr>
<tr>
<td></td>
<td>PTS</td>
<td>100</td>
<td>0.009 (0.002)</td>
<td>0.996 (0.010)</td>
</tr>
<tr>
<td>200</td>
<td>BTS</td>
<td>100</td>
<td>0.011 (0.001)</td>
<td>1.01 (0.011)</td>
</tr>
<tr>
<td></td>
<td>PTS</td>
<td>200</td>
<td>0.005 (0.001)</td>
<td>0.877 (0.008)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>100</td>
<td>0.008 (0.001)</td>
<td>0.988 (0.009)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>200</td>
<td>0.004 (0.001)</td>
<td>0.865 (0.009)</td>
</tr>
</tbody>
</table>

* Truncation selection on BLUP estimated breeding values (BTS) or phenotypic (PTS) values.
In general, BTS schemes resulted in higher $\Delta F$ and $\Delta G$. $\Delta F$ could especially be increased with up to two to three times the $\Delta F$ of PTS, whereas the increase in $\Delta G$ was smaller. For traits with high heritability, $\Delta F$ of the BTS schemes was markedly lower but still higher than the corresponding PTS scheme.

4. Discussion

When going from PTS to BTS, we found an overall increase of $\Delta G$ and $\Delta F$ of a factor of 0.07 and 1.45, respectively (Tables 1 and 2). Hence, the increase of $\Delta G$ was moderate and accompanied by a dramatic increase of $\Delta F$. In fact, most BTS schemes resulted in much too high rates of inbreeding ($\geq 0.01$) for typical fish breeding schemes, which are quite large in terms of number of selection candidates, symmetrical with respect to the number of selected sires and dams and limited by the number of tanks that the nucleus has. Truncation selection on phenotypic values achieved a $\Delta F$ of 0.01 or less, which is the generally recommended rate of inbreeding per generation (e.g., see Goddard, 1992).

One possibility to reduce $\Delta F$ would be to select more parents than we did in these schemes. However, because of the limited number of tanks, this is not possible. Hence, for BTS schemes constrained by 100 tanks and 3200 or 6400 selection candidates, 100 selected sires and dams are too few to obtain an acceptable rate of inbreeding (i.e., $\Delta F=0.01$ or less). For BTS schemes constrained by 200 tanks, 200 selected sires and dams are too few when selection is practiced for a trait with low heritability and a minimum when selection is practiced for a trait with medium to high heritability.

Another option to reduce $\Delta F$ in BTS schemes is to limit the number of fish selected per family. We have not considered this option here because very many combinations of total number of selection candidates, number of selected fish and maximum number of selected fish per family are possible. The problem to find the optimum solution is even larger if we vary the number of fish selected per family, e.g., 10 from the best family, 8 from the second best, etc., i.e., departing from the truncation selection strategy.

Results of this study show that the number of selection candidates and tanks is critical to the $\Delta F$, i.e., the risk of the breeding scheme, although $\Delta F$ and $\Delta G$ were more affected by the heritability and number of selected parents than by the two constraints studied. For a given number of selection candidates, a low number of tanks (i.e., large family size) increases $\Delta F$. Similarly, for a given number of tanks, a high number of selection candidates (i.e., large family size) increases $\Delta F$. However, the effects of these constraints on $\Delta F$ were smaller for the BTS than the PTS schemes. For the BTS schemes, effects were larger for schemes with low heritability of 0.1. To obtain the same $\Delta F$ for a given number of selection candidates, a higher number of families or tanks (i.e., smaller family size) are needed for BTS than for PTS particularly for schemes with low and medium heritability. The effect on $\Delta G$ of the two constraints was small for both BTS and PTS.

An advantage with PTS schemes is that they are less costly to run than BTS schemes, where family groups need to be kept in different tanks until they can be tagged. In PTS schemes, fish from all families can be reared in only one tank from the time of fertilization. Hence, the common environment effect (i.e., tank effect) will be zero, such that no tank effect needs to be estimated. However, for current sib-selection breeding schemes, the common environment effect (including, e.g., tank, maternal, nonadditive and epistatic effects) is often small, such that the advantage of PTS schemes is reduced. For example, in Atlantic salmon and rainbow trout populations, the common environment effect (i.e., tank effect) on growth rate was estimated to be about 2–6% (Rye and Mao, 1998; Pante et al., 2002). For more recently domesticated species where the environment is not yet standardized, the common environment effect can still be rather large. In cod (Gjerde et al., in press), the common environment effect on juvenile body weight was estimated to be 3–12%, and in rohu carp, this effect (i.e., nursery pond effect) on harvest body weight was 32% (Gjerde et al., 2003).

The greatest disadvantage of PTS schemes is that the trait has to be measured on the candidate itself because each fish is not individually identified. Today, many practical breeding schemes start out with selecting only for one trait (growth) or a limited number of traits that can be recorded on the candidate, but more advanced schemes select for more traits like fillet quality and disease resistance.
traits that can only be measured on sibs of the candidates. For these schemes, BTS selection is preferred because it can take account of sib information. It is not known today how PTS compares with BTS for schemes where several traits can be measured on the candidate, and the genetic covariance between the traits is unknown due to lack of pedigree information. These covariances could, however, be obtained from other populations, with the risk that they are not valid in the current population.

Results are in accordance with other studies on design of PTS schemes for fish (Gjerde et al., 1996; Villanueva et al., 1996; Bentsen and Olesen, 2002) and comparisons of PTS and BTS (e.g., see Quinton et al., 1992; Quinton and Smith, 1995; Gjoen and Gjerde, 1998). In the fish schemes simulated here, which are quite large in terms of number of selection candidates but with a relatively low number of families and symmetric with respect to the number of selected sires and dams, BTS often resulted in higher rates of inbreeding than in the study of Quinton et al. (1992), such that the graphs of PTS and BTS hardly overlap here (Fig. 1a and b) at least for schemes with low and moderate levels of heritability. For the size of schemes that we considered here, BTS would result in much too high $\Delta F$ than can be acceptable in practical breeding schemes. The problem with truncation selection for BLUP breeding values is the correlation of breeding values within families, such that relatively few families are selected and rate of inbreeding increases (Wray and Thompson, 1990). There are group selection methods that maximise genetic gain with a restriction on the rate of inbreeding for schemes with discrete (Meuwissen, 1997; Grundy et al., 1998) or overlapping generations (Meuwissen and Sonesson, 1998; Grundy et al., 2000). They are dynamic, such that they adapt to current selection candidates and can therefore correct skewness in contribution of families over generations. Skewness of contributions of families results in higher rate of inbreeding. These optimum contribution methods have been shown to increase genetic gain with up to 44% compared to BTS schemes at the same rate of inbreeding for livestock schemes. However, these group selection methods are computationally very demanding for large numbers of selection candidates.

4.1. Relaxation of assumptions

In this study, we considered a ratio of numbers of selected sires to dams ($R$) of 1.0 and random mating among the selected fish. An $R$ of 1.0 is theoretically ideal because any distortion in contributions within or over families increases rates of inbreeding. However, for reasons other than rates of inbreeding, e.g., to be able to account for the tank effect for BLUP estimated breeding values, $R$ is often 2.0 in practical breeding schemes. For schemes with $R=2.0$, the inbreeding problem is expected to be higher, and thus, rates of inbreeding would be even less acceptable.

We assumed that the number of family groups (i.e., tanks) was limited to 100 or 200, whereas the smallest scheme considered only five selected sires and dams, i.e., $5 \times 5=25$ matings if all possible matings were done. Therefore, when selecting a low number of parents, certain sires and dams will be mated more frequently but not necessarily to the same partner. In practical schemes, repeated matings will probably not take place frequently, but the aim of this paper was to study the effects of selection and not mating. Therefore, random mating was applied in this study.

We assumed that not only the BTS schemes but also the PTS schemes were limited by a certain number of tanks. In practice, this is not necessarily the case for PTS schemes, which makes the PTS scheme less costly to run than the BTS scheme. However, if one is concerned with the actual contribution of each selected parent, it is reasonable to assume a controlled mating system like what we use here also for the PTS schemes. For PTS schemes, pooling of a given number of individuals from each family group could take place at fertilization or shortly thereafter but should preferably be delayed, for example, to the time of first feeding, to eliminate different fertilization, hatchability and survival rates among the families. This is particularly important for species with high mortality rates at egg and larvae stages. A special BTS scheme where costs of rearing the fish until tagging will be the same as for PTS schemes is when candidates are pooled at fertilization or shortly thereafter, and DNA fingerprinting is used to assign offspring to parents. After tagging, the cost of rearing fish is the same for BTS and PTS. Hence, the restriction on the number of candidates does not affect the cost of the breeding scheme after tagging.
We did not account for inbreeding depression in this study because we assumed additive inheritance of the trait that we selected for. However, for traits affected by inbreeding depression, i.e., traits with dominant inheritance, effects of inbreeding depression on $\Delta G$ should be accounted for. This negative effect on $\Delta G$ will be larger for BTS than PTS inasmuch as the BTS schemes had a higher $\Delta F$ than the PTS schemes. At low rates of inbreeding (1% per generation), inbreeding depression in growth was below 5% per 10% increase in inbreeding coefficient (Rye and Mao, 1998; Pante et al., 2001). This reduction in $\Delta G$ will be in favour of the PTS scheme but will not change the main conclusions in this study.

5. Conclusions

For large scale fish selection schemes that only select for one trait with low to middle heritability, PTS gives lower rate of inbreeding and equal or higher genetic gain than BTS, which often had unacceptable high rate of inbreeding ($\geq 0.01$). To obtain the same $\Delta F$ for a given number of selection candidates, a higher number of families or tanks (i.e., smaller family size) are needed for BTS than for PTS, in particular, for schemes with low and medium heritability. However, PTS can only be used for traits measured on the selection candidate itself, which makes PTS less valuable for fish breeding schemes with comprehensible breeding goals, where several traits can only be measured on sibs. One should, however, be cautious with the use of BTS schemes because rates of inbreeding can easily exceed the acceptable rates by a factor two or more.

6. Uncited reference

Falconer and Mackay, 1996

Acknowledgements

This study was financially supported by Norwegian Research Council grant 139630/140.

References


