The use of alternative breeding schemes to enhance genetic improvement in rainbow trout (*Oncorhynchus mykiss*): I. One-stage selection

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Abstract

The rates of genetic gain and inbreeding were examined in alternative breeding designs of rainbow trout with different mating ratios, variable number of individuals measured and different number of traits included in a selection index in a closed nucleus-breeding scheme. Three body weight records during growth at the nucleus central station and body weight before marketing at a separate sea station (the breeding objective) were assumed to be recorded, and the genetic parameters were obtained from the actual Finnish breeding program. The rates of genetic gain were determined using the prediction error variance–covariance matrix of the traits included into the best linear prediction of breeding values. The rates of inbreeding were calculated using a first-order approximation, by empirically obtaining the probabilities of co-selection of relatives. The analysis showed that the rate of genetic gain can be improved as much as 20% by changing the mating ratios from the traditional nested designs (e.g., ratio of sires to dams 1M : 3F) to factorial mating (e.g., 3M : 5F). This enhance in genetic gain is mainly due to an increase in the selection intensity of females, which is constant in the nested designs with a fixed number of full-sib family tanks for a given family size. The rates of inbreeding appear to be higher for factorial than for nested designs, although, at the same rate of inbreeding, factorial designs present equal or higher rates of genetic gain compared to nested designs. The accuracy of the breeding values differ only little among the different mating ratios explored, whereas the inclusion of information from relatives at the sea station in the selection index increased the accuracy, and thus, the genetic gain.

1. Introduction

The use of different mating systems and different selection criteria exert a major influence on the response to selection in breeding programs. It has been shown previously that modifications of the designs of breeding programs play a key role in increasing selection response (e.g., Grundy et al., 1994, 1998; Villanueva and Woolliams, 1997, and references therein), especially

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when techniques to increase the number of offspring per female are being used (Woolliams, 1989; Ruane, 1991). However, similar studies in the field of fish breeding are rare. Recently, Gjerde et al. (1996) and Villanueva et al. (1997) examined optimal designs of fish programs in a population undergoing mass selection for a single trait. In practice, breeders utilize multiple traits in the selection index (that can or cannot be measured on the available candidates of selection) to improve several traits because of their influence on the profitability. Construction of genetic indices, using best linear unbiased predictors (BLUP, Henderson, 1984), is a way to simultaneously handle multiple traits and pedigree information. Such indices give larger response to selection in the short to medium term.

Studies aimed at optimizing designs of breeding programs of other farm animals are not directly applicable to fish breeding because, in contrast to many domesticated animals, female fish have external fertilization and extremely high reproductive capacity (one female can produce thousands or millions of eggs), allowing several alternative breeding designs to be applied. In addition to different mating ratios, high reproductive capacity of females provides an opportunity to apply selection in stages (e.g., during early life and at spawning) and testing large number of sibs of breeding candidates for their performance (e.g., growth in different environments or disease resistance). Information from the breeding candidates and their sibs tested at the test stations together with pedigree information can be further combined into a genetic index that ranks the breeding candidates. All these facts motivated us to deterministically examine the benefits of alternative breeding designs in the Finnish breeding program of rainbow trout b (Walbaum).

In Finland, more than 80% of the commercial rainbow trout populations are reared in net cages in the Baltic Sea, and the main trait of interest in commercial aquaculture is body weight before maturation at the sea. The breeding program, on the other hand, consists of a fresh water central station where the breeding candidates are held, and seawater stations where the performance of full and half sibs of the breeding candidates are tested. A significant genotype-by-environment interaction for growth rate has been reported (Kettunen et al., 1999; Kause et al., 2003). Therefore, the selection criteria must incorporate information not only from the central station itself, but also from the test stations where the actual genetic improvement needs to be realized. This is especially important because phenotypic information on the breeding objective (body weight of 2-year-old fish) cannot be obtained from the selection candidates. Moreover, a traditional paternal nested mating design has been applied in the program, but recent studies indicate that factorial designs may be more suitable (Woolliams, 1989; Berg and Henryon, 1998).

In the present paper, deterministic simulations are utilized to examine the factors that contribute to the expected rates of genetic gain in alternative breeding designs. We specifically studied different mating ratios, different number of individuals measured and different number of traits included in a selection index. In addition to genetic gain, the asymptotic rates of inbreeding in the alternative designs are predicted using a first order approximation (Woolliams, 1989).

2. Material and methods

2.1. Alternative breeding designs studied

The Finnish breeding program was initiated in the late 1980s. Breeding candidates are held at the Tervo Fisheries Research and Aquaculture station (a fresh water station) and their full sibs are tested at commercial fish farms situated at the Baltic Sea (brackish water stations). The generation interval in the scheme is three years. The complete breeding cycle is depicted in Appendix 1, and the program is detailed by Kause et al. (2005). Here we describe the alternative breeding designs that were examined in the deterministic simulation.

2.1.1. Construction of selection indices

The traits under selection are assumed to be genetically controlled by an infinite number of unlinked loci each with a small effect, i.e., the infinitesimal model (Bulmer, 1980; Martinez et al., 2000). The population is assumed to have an equal sex ratio, to follow discrete generations with selected parents mated at random, and to be structured according to the mating designs presented in Table 1.

Four different body weight records were assumed to be available for predicting the breeding values (BV) for the traits included in a selection index. At the central station, body weight can be recorded after the first growing season when individuals are tagged (BW_I) and after the first pond growing season (BW_{II}) and after the second pond growing season (BW_{III}). Body weight of the sea ranched fish is recorded after the second growing season (BW_{IV}), just before the fish are slaughtered and marketed. Accordingly, alternative selection indices can include any combination of the four traits (BW_I, BW_{II}, BW_{III} and BW_{IV}).

Table 1
Mating schemes (ratio of males and females, M:F) utilized in the alternative breeding schemes for 200 and 300 family tanks available

Mating design	Number of tanks			
	200		300	
	Sires	Dams	Sires	Dams
Factorial				
2M:2F	100	100	150	150
2M:3F	66	99	100	150
2M:4F	50	100	74	148
2M:5F	40	100	60	150
3M:3F	66	66	99	99
3M:4F	48	64	75	100
3M:5F	39	65	60	100
Nested				
1M:3F	66	198	100	300
1M:4F	50	200	75	300
1M:5F	40	200	60	300
1M:6F	33	198	50	300
1M:7F	28	196	42	294

Additive genetic and residual variance–covariance matrices of the traits studied are needed in the estimation of breeding values and genetic gains. The parameters used for the simulations (Tables 2 and 3) were those estimated from the actual breeding program (Kettunen et al., 1999). The population has been under mass selection for improved growth rate before the genetic parameters were estimated. Therefore, it is likely that the parameters have already reached their asymptotic values due to linkage disequilibrium, i.e., the Bulmer effect (Bulmer, 1980). Furthermore, previous studies have shown that the ranking of different breeding designs using either one generation methods or algorithms that account for decrease in genetic variance due to linkage disequilibrium do not differ greatly, and that the one generation

Table 2
Mean, phenotypic standard deviation (σ_p), additive standard deviation (σ_a), common environmental standard deviation (σ_c) and residual standard deviation (σ_e) of body weights (BW$_{I-IV}$) (from Kettunen et al., 1999)

Trait	Mean	σ_p	σ_a	σ_c	σ_e
BW$_I$	47	16	10	5	11
BW$_{II}$	717	199	122	0	157
BW$_{III}$	2665	552	333	0	440
BW$_{IV}$	822	219	103	0	193

All traits are expressed in grams as units of measurement.
BW$_I$=body weight in fresh water at tagging; BW$_{II}$=body weight in fresh water after two growing seasons; BW$_{III}$=body weight in fresh water after three growing seasons; BW$_{IV}$=body weight in sea water after two growing seasons.

Table 3
Genetic parameters for body weights (BW$_{I-IV}$) included in the analyses

	BW$_I$	BW$_{II}$	BW$_{III}$	BW$_{IV}$
BW$_I$	0.38	0.58	0.33	0.50
BW$_{II}$	0.36	0.38	0.82	0.56
BW$_{III}$	0.27	0.81	0.36	0.42
BW$_{IV}$	ne	ne	ne	0.22

Heritabilities (diagonal), genetic correlations (upper diagonal) and residual correlations (below diagonals) are given.
ne=non-estimable; BW$_I$=body weight in fresh water at tagging; BW$_{II}$=body weight in fresh water after two growing seasons; BW$_{III}$=body weight in fresh water after three growing seasons; BW$_{IV}$=body weight in sea water after two growing seasons.

method is adequate to compare breeding schemes (Mueller and James, 1984; Wray and Hill, 1989).

Selection indices are based on the information recorded from the breeding candidates themselves, parents of the candidates, and from full and half sibs of the candidates. To construct the genetic indices, multi-trait best linear unbiased predictors (BLUP) were calculated by the following general model that includes all the information to construct the genetic indices (see below):

$$
\begin{bmatrix} y_1 \\ . \\ . \\ y_4 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & & 0 \\ & . & \\ & & . \\ 0 & & \mathbf{X}_4 \end{bmatrix} \begin{bmatrix} b_1 \\ . \\ . \\ b_4 \end{bmatrix}
$$
$$
+ \begin{bmatrix} \mathbf{Z}_1 & & 0 \\ & . & \\ & & . \\ 0 & & \mathbf{Z}_4 \end{bmatrix} \begin{bmatrix} a_1 \\ . \\ . \\ a_4 \end{bmatrix}
$$
$$
+ \begin{bmatrix} \mathbf{W} & & 0 \\ & . & \\ & & . \\ 0 & & 0 \end{bmatrix} \begin{bmatrix} c \\ . \\ . \\ 0 \end{bmatrix} + \begin{bmatrix} e_1 \\ . \\ . \\ e_4 \end{bmatrix} \quad (1)
$$

where y_i is a vector of observations for a ith trait (BW$_I$, BW$_{II}$, BW$_{III}$ and BW$_{IV}$) included in a selection index, b_i is a vector of fixed effects, a_i is a vector of breeding values (BV) for a ith trait of an animal k, c is a vector of common environmental effects for body weight after one growing season at the central station (BW$_I$), and e_i is a vector of residuals corresponding to each trait. $\mathbf{X}_i$, $\mathbf{Z}_i$ and $\mathbf{W}$ are the corresponding incidence matrices relating the random variables and the observations. Although this model includes all four traits, only the traits included in the respective selection index were used each time (described by Eq. (4)). For the purpose of calculations of genetic gains, fixed effects were assumed to be known, and therefore, only random effects were predicted.

The variance–covariance structures for a_i, c_i, and e_i needed in the Eq. (1) are equal to:

$$\mathrm{Var}\begin{bmatrix} a_{1..4} \\ c \\ e_{1..4} \end{bmatrix} = \begin{bmatrix} \mathbf{A} \otimes \mathbf{G}_{11} & 0 & 0 \\ 0 & \mathbf{I}\sigma_c^2 & 0 \\ 0 & 0 & \mathbf{I} \otimes \mathbf{R} \end{bmatrix} \quad (2)$$

where $\mathbf{A}$ is the numerator relationship matrix, $\mathbf{G}_{11}$ is the additive genetic variance–covariance matrix for all the traits included in the selection criteria (Kettunen et al., 1999), $\otimes$ is the Kronecker product, σ_c^2 is a variance of common environmental effects for BW_I, $\mathbf{R}$ is a variance–covariance matrix of residual effects with zero covariance for traits measured on different individuals (i.e., between individuals raised at the nucleus and the sea station) and $\mathbf{I}$ is an identity matrix. Given these premises, the equations of the multi-trait random models (Eq. (1)) can be solved following Henderson (1984).

For each individual, genetic indices are computed as the product of the breeding values of each trait used in a selection index and the vector of the genetic regression coefficients between these predictors and the selection objective. The vector of genetic regressions coefficients ($b_{\mathrm{Ig}(i)}$) for the ith genetic index is computed following Henderson (1977) and Schneeberger et al. (1992) as:

$$b_{\mathrm{Ig}(i)} = [\mathbf{G}_{11}^{-1}\mathbf{G}_{12}]'\nu \quad (3)$$

where $\mathbf{G}_{12}$ is a variance–covariance matrix between the breeding values of the traits included in a selection index and the breeding objective, and ν is a vector of economic weights for the traits included in the breeding objective, which is the general case of a breeding objective incorporating more than one trait. Note that in the present study ν is a scalar because only a single trait is included in the breeding objective.

Three genetic selection indices were used to find the best breeding candidates among the animals available:

$$\mathrm{Ig}(1) = b_1\mathrm{PBV}(BW_I) + b_2\mathrm{PBV}(BW_{IV})$$

$$\mathrm{Ig}(2) = b_1\mathrm{PBV}(BW_I) + b_2\mathrm{PBV}(BW_{II}) + b_3\mathrm{PBV}(BW_{IV})$$

$$\mathrm{Ig}(3) = b_1\mathrm{PBV}(BW_I) + b_2\mathrm{PBV}(BW_{II}) + b_3\mathrm{PBV}(BW_{III}) + b_4\mathrm{PBV}(BW_{IV}). \quad (4)$$

For example, the index Ig(1) for an individual is obtained as the product of the genetic regression coefficients b_1 and b_2 and the predicted breeding values (PBV) (using Eq. (1)). These PBVs were obtained including phenotypic information of BW_I from the breeding candidates, their parents, and their half and full

sibs reared at the central station, and including information of BW_{IV} from different numbers of half and full sibs reared at the sea station. Note, however, that the vector of genetic regressions has only non-zero elements at the weight given by the predicted breeding values for BW_{IV}.

2.1.2. Mating ratios

In each spring, 3-year-old fish are selected and allowed to produce the next generation, and both nested and factorial mating designs can be easily produced. In paternal nested designs, each sire is mated to several dams but each dam is utilized only once. In factorial mating, each sire is mated to several dams and each dam is mated to several sires. Table 1 shows the nested and factorial mating ratios utilized in the present study.

2.1.3. Family size

After 4 weeks of incubation, eye-stage eggs are transferred into indoor 150-l tanks (one full-sib family per tank). During the first growing season, the number of fingerlings in each tank can be as high as 500 individuals, but the following autumn family size is cut down to 175 fingerlings, so this value was used as the maximum family size.

After 6 months of growing (Appendix 1), fingerlings are large enough (about 50 g) to be tagged randomly with passive integrated transponders. After tagging each full-sib family is split into two groups to be reared at the central station and at the sea station. To create alternative breeding designs for the deterministic simulations, a total of 16, 24, 32, 40 and 50 individuals per full-sib family were assumed to be recorded for performance testing from the beginning of the production cycle at the central station, and 0, 7, 15, 20, 25 and 30 individuals per full-sib family for testing at the sea station.

2.1.4. Calculation of genetic gain

The following calculations comprise only information given by the accuracy of predicted breeding values for BW_{IV}, i.e., the breeding objective (H). When selection is by truncation on index values, the rate of genetic gain per generation (ΔG in units of genetic standard deviations) in the breeding objective is predicted by:

$$\Delta G = i\rho_{\mathrm{Ig}(i),H} = i\frac{\sigma_{\mathrm{Ig}(i)}}{\sigma_H} \quad (5)$$

where $i = (i_{\mathrm{males}} + i_{\mathrm{females}})/2$ is the mean selection intensity of males and females, $\rho_{\mathrm{Ig}(i),H}$ is the correlation of the ith index and the selection objective (i.e., accuracy of prediction of breeding values for BW_{IV}), and σ_H is a

standard deviation of the selection objective. $\sigma_{\mathrm{Ig}(i)}$ is a standard deviation of the index and is computed as:

$$\sigma_{\mathrm{Ig}(i)} = \sqrt{\mathrm{Var}(\mathrm{PBV_{BWIV}})} \qquad (6)$$

and

$$\mathrm{Var}(\mathrm{PBV_{BWIV}}) = [a_{kk}\mathbf{G}_{11} - \mathbf{C}_{kk}] \qquad (7)$$

where a_{kk} is a coefficient of the numerator relationship matrix for the kth candidate with itself (equal to 1). $\mathbf{C}_{kk}$ is a variance–covariance matrix of prediction errors of traits for the kth animal (Henderson, 1984). This matrix was extracted directly after inverting the left hand side of the coefficient matrix of the mixed model equations given the information included as selection criteria (Henderson, 1984).

Selection intensities were computed assuming a fixed number of tanks available for keeping full-sib groups separately during the first stages of growth, with a variable number of individuals available within these tanks for selection at spawning. Note that the selection intensity is only dependent on the number of candidates for selection per tank and independent of the number of tanks available at the beginning of the life cycle. Mortality rates affect selection intensity and the accuracy of predicted breeding values in different ways. Selection intensity depends on the number of candidates of selection surviving from tagging until spawning. Since mortality is sequential throughout the life cycle (about 16% from BW_I and BW_{II}, 24% between BW_{II} and BW_{III}) and 25% between BW_{II} and BW_{IV} (when body weight is measured at the sea station) measurements can only be made on survivors at each measurement when different traits are included in the selection criteria. The expected number of survivors due to random mortality at each stage is accounted for when calculating the accuracy of predicted breeding values.

2.2. Assessment of the rates of inbreeding

We calculated a first-order approximation of the rates of inbreeding for the different mating designs described previously (Section 2.1.2). The theory behind the prediction of the rates of inbreeding under univariate BLUP-selection has been considered recently by Bijma and Woolliams (2000). In the present paper, we derive empirically the estimated rates of inbreeding (ΔF) by calculating the effective population size under selection using transition matrices to describe the probability that the genes chosen from selected individuals in a given generation are identical by descent (Bartlett and Haldane, 1935; Woolliams, 1989; Wray et al., 1990; Villanueva and Woolliams, 1997).

The calculation of inbreeding is based on the probabilities of co-selection of relatives. These probabilities were obtained empirically (i.e., the probabilities of co-selection full, or half sibs) following the expressions derived by Burrows (1984) and by simulating the different breeding programs presented in Table 1. For these calculations 50 and 10 full sibs were assumed to be recorded at the central station for BW_I and at the sea station for BW_{IV}. From the candidates available for selection, individuals were selected based on the breeding values for the breeding objective (BW_{IV}; Eq. (1)) using index Ig(2). The ΔF values for the different breeding programs were obtained using a function of the maximum eigenvalue of a transition matrix that describes all paths by which probabilities of identity by descent can be calculated (see Woolliams, 1989 for a detailed explanation). Using this method, it was expected that the ranking of the different breeding designs in terms of the rates of inbreeding would not differ compared to ranks obtained using more cumbersome methodology. Still, similar results have been found using this method compared to simulations of breeding programs under mass selection (Wray et al., 1990). The results are presented using the average ΔF of 100 replicates for each design and mating ratio evaluated.

3. Results

3.1. Genetic gain

3.1.1. Selection indices constructed for predicting breeding values

The results showed that the different selection indices exert a major influence on the accuracy of predicted breeding values of the breeding objective (BW_{IV}). Similar results were observed irrespective of the mating designs and the number of individuals recorded for each trait. Thus, general results for the differences between the indices are presented here, and examples are presented to illustrate the results.

Switching from index Ig(1), which includes information on BW_I and BW_{IV}, to index Ig(2), including BW_I, BW_{II} and BW_{IV}, improved accuracy considerably (data not shown). For instance, applying the indices Ig(1) and Ig(2) in a factorial 3M:5F design with 16 fish recorded for BW_I per family resulted in about 7% increase in the accuracy (from 0.45 to 0.52).

Inclusion of BW_{III} in the selection index (the index Ig(3)) did not noticeably improve the accuracy, and thus, the rates of genetic gain (data not shown). This result is expected because the genetic correlation between BW_{III} and BW_{IV} (0.42) is lower than the genetic correlation

between BW_{II} and BW_{IV} (0.56; Table 3). Thus, BW_{III} contributes very little added information to predict BW_{IV}.

3.1.2. Mating ratios

Because the accuracy of predicted breeding values increased only little when including BW_{III} in the Ig(3) selection index, only the results for the index Ig(2) are presented hereafter.

The genetic gain in the breeding objective was higher in the factorial mating designs compared to the nested designs (Figs. 1 and 2). For instance, when selection index Ig(2) was utilized, genetic gain was 11–25% higher for factorial design 3M:5F compared to nested design 1M:3F (Fig. 1B). This was consistent with the results of the Monte Carlo simulation to obtain the asymptotic rates of inbreeding (see Table 4). At the same rate of inbreeding, however, genetic gains of factorial designs were slightly higher or similar to those of nested designs. For example, the factorial designs 2M:2F yielded negligible differences in genetic gain with nested 1M:5F (from −0.01% to 0.02%), while factorial designs 2M:4F yielded about 6% higher rates of genetic gain with nested 1M:6F to gains (Fig. 1A and Table 4).

The higher genetic gains of the factorial designs are explained mainly by their higher selection intensities compared to the nested mating designs. In the paternal nested mating designs, each male is mated with several dams whereas each dam produces only one family. Thus, 200 females are needed to realize a nested mating design with a fixed number of 200 family tanks, and selection intensity of females remains constant irrespective of the mating ratio (Fig. 3). The use of a factorial mating design reduces the number of females needed to produce the next generation, and thus, selection intensity is increased (Fig. 3). The accuracy of the breeding values is only slightly higher for the factorial designs (Fig. 4), thus contributing very little to the difference in the genetic gains between the mating designs.

A reader should note that in nested designs the total number of females is the same for a fixed number of tanks, thus selection intensities of females are the same for different mating ratios used. For factorial designs, female selection intensities differ only when either 2 or 3 males are mated to a variable number of females within the mating set (see Table 1 and Fig. 3).

3.1.3. Family size

As explained in the previous sections, genetic gain depends on the number of individuals recorded at the

beginning of the life cycle (when calculating accuracy estimates) and at spawning (when calculating selection intensity). For this reason, the results show that in all mating designs, an increase in a number of breeding candidates reared at the central station (range being 16–50 individuals tagged and recorded for BW_I at the beginning of the life cycle) increased the genetic gain in the breeding objective, BW_{IV}.

The observed increase in ΔG as a function of the number of individuals recorded per family at the central station (Fig. 2) resulted mainly from the increase in the selection intensity (Fig. 3) and to a lesser extent from the increase in accuracy (Fig. 4). For example, when increasing the number of individuals recorded per family for BW_I from 16 to 50, the mean selection intensity increased about 20% (Fig. 3), whereas increases in the accuracy were negligible (Fig. 4). The increase in ΔG as a function of the number of individuals recorded at the sea station for BW_{IV} (Fig. 2), on the other hand, was a direct result of an increase in the accuracy (Fig. 4), because individuals reared at the sea station were not breeding candidates, and thus, their number did not influence selection intensity.

When the breeding program relies only on the information from the central station (zero individuals were tested at the sea station), genetic response in the breeding objective is relatively low (Fig. 2). The improvement in genetic gain, when including information from the sea station for BW_{IV} can be as large as 20% compared with zero individuals tested at the sea station. The improvement in the accuracy levels out when the number of individuals tested at the sea station increases from 7 to 20 individuals recorded per family (Fig. 4).

3.2. Assessment of the rates of inbreeding

Rates of inbreeding are presented for a design in which 50 and 10 individuals were recorded for BW_I and BW_{IV}, respectively (Table 4). For both the nested and factorial designs, the rates of inbreeding increased linearly with increasing mating ratios, due to the increase in selection intensity. It appeared that factorial mating designs gave generally higher rates of inbreeding compared to the nested designs, as a consequence of the higher selection intensities realized when factorial mating were used. For factorial designs, the approximated values of ΔF per generation ranged from 0.028 (2:2) to 0.049 (3:5) for 200 tanks. For nested designs, the values ranged from 0.019 (1:3) to 0.035 (1:7) (Table 4). Note that increasing the testing capacity from
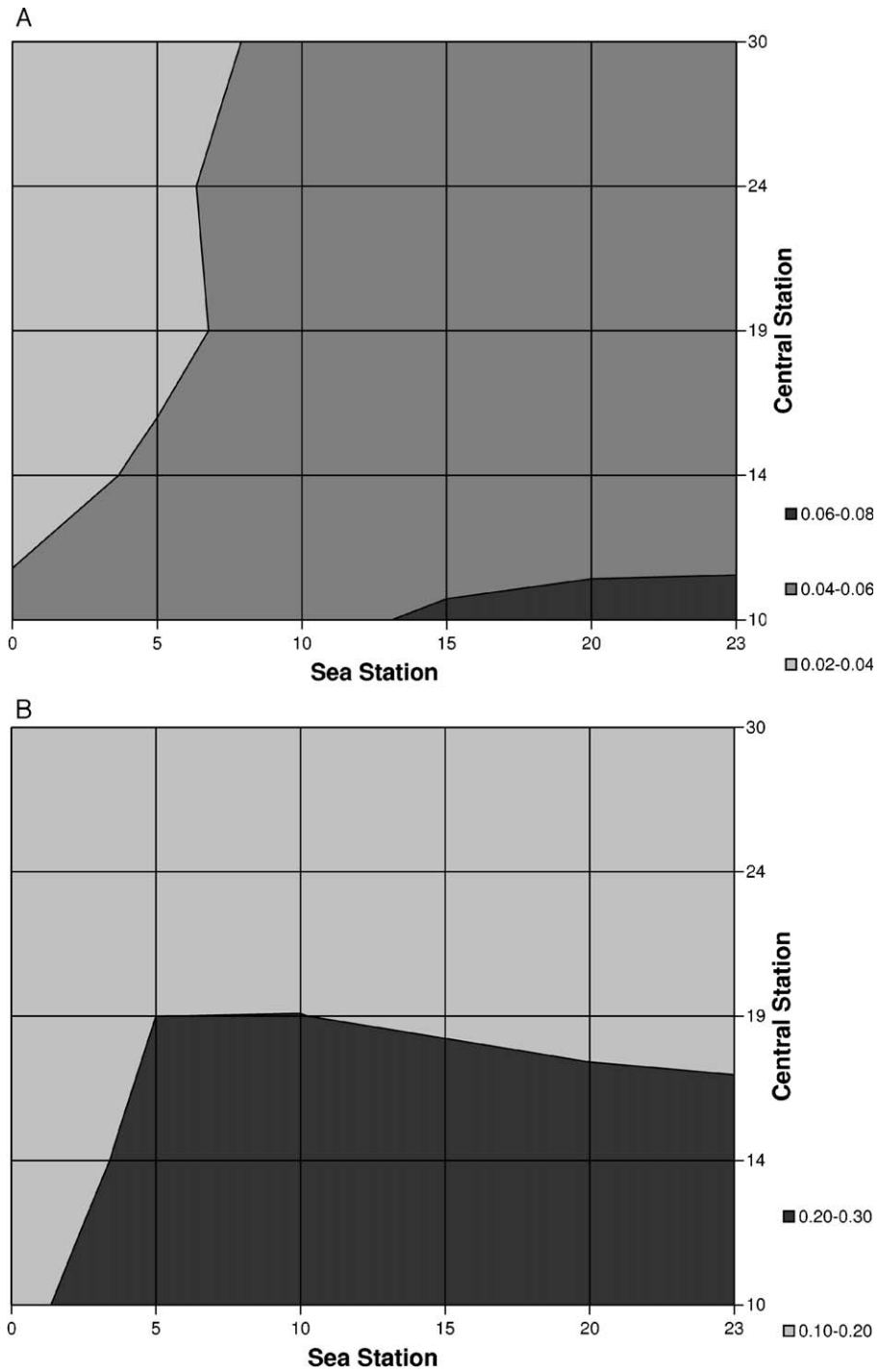
Fig. 1. Contour plots showing the relative efficiency (%) of factorial designs over the nested designs in terms of genetic gain. The results are presented for different number of individuals recorded per full-sib family at the central (*Y* axis) and at the sea station (*X* axis). (A) Shows the relative efficiency for 2M:4F versus 1M:6F (at the same rate of inbreeding) and (B) for 3M:5F versus 1M:3F for different rates of inbreeding. Selection index Ig(2) was used in all cases.
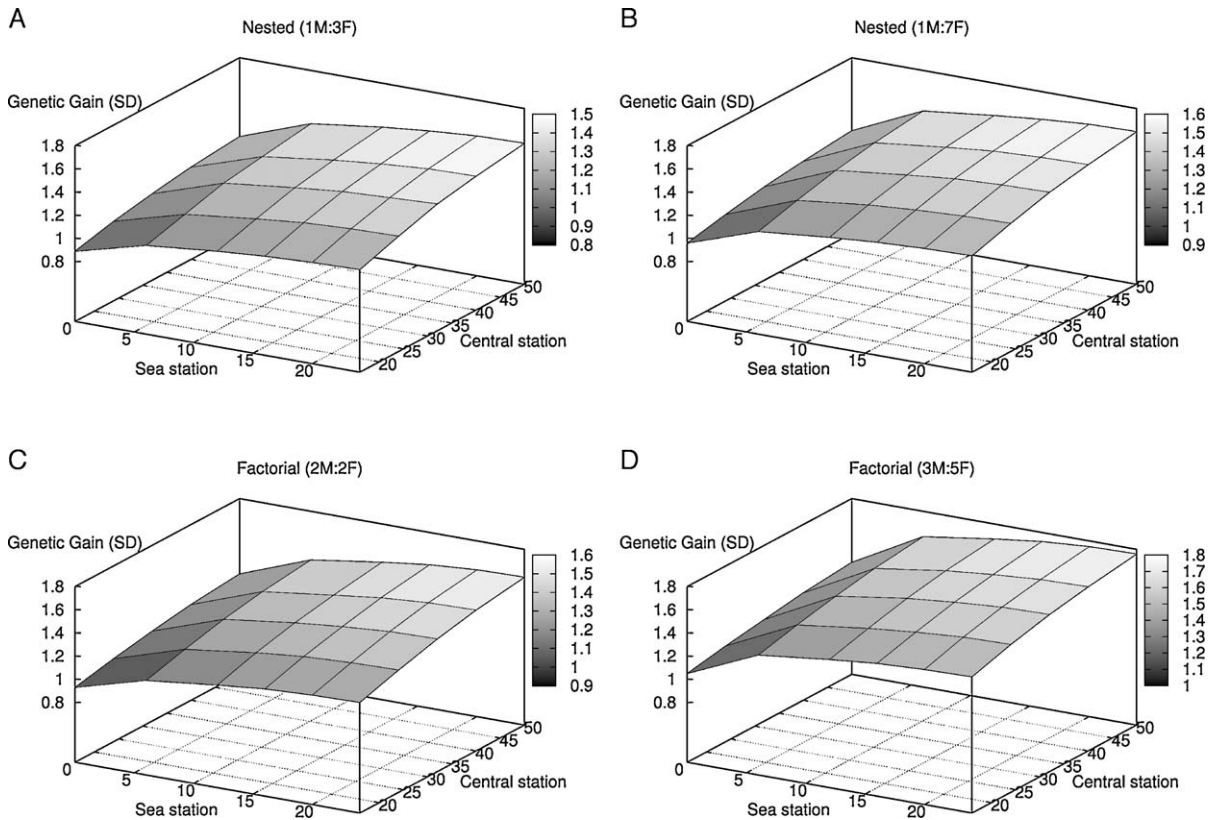
Fig. 2. Effect of the number of individuals recorded at the central (*Y* axis) and the sea station (*X* axis) on the rates of genetic gain (*Z* axis) in the breeding objective according to different mating designs. Selection index Ig(2) was used in all cases.

200 to 300 tanks considerably reduced the rates of inbreeding (Table 4).

4. Discussion

The present paper examined the rates of genetic gain and inbreeding in alternative breeding designs with different mating ratios (nested or factorial), different number of individuals measured, and with different number of traits included in the selection index. The Finnish breeding program for rainbow trout was utilized as a model system. The objective was to decompose the factors that explain the differences in the genetic gain under realistic scenarios among the alternative breeding designs, and with this information, to develop breeding programs that efficiently make use of all the information.

To study the expected gains in the breeding objective, we used all the available information from the pedigree and multiple traits from a real breeding program. Previous papers on the optimization of fish breeding programs have considered mass selection on a single normally distributed trait (Villanueva et al., 1997; Gjerde et al., 1996; Bentsen and Olesen, 2002). Mass

selection schemes can only be applied in situations where broodstock can be measured directly for traits in the breeding objective. For example the methods of Villanueva et al. (1997) and Gjerde et al. (1996) maximize genetic gains for a fixed rate of inbreeding under mass selection. In breeding programs with pedigreed populations, a breeder is interested in using all the information available from multiple traits to improve genetic gain. Our approach was to maximize genetic gains under constrained resources (i.e., number of individuals tagged) when breeding candidates cannot be measured for the breeding objective. Under these circumstances, pedigree is needed for predicting breeding values for the breeding objective, which seems to be a more realistic scenario in modern breeding schemes. Further research is needed to optimize this type of breeding program for fish using multi-trait BLUP-selection under restricted rates of inbreeding.

4.1. Genetic gains in alternative breeding designs

The use of factorial mating designs has been proposed to enhance the genetic gain in closed nucleus

Table 4
Genetic gain (ΔG in genetic standard deviation units) and rates of inbreeding (ΔF) accounting for selection in a breeding program using 200 and 300 family tanks

Mating design	Number of tanks			
	200		300	
	ΔG	ΔF	ΔG	ΔF
Factorial				
2M:2F	1.38	0.028	1.36	0.020
2M:3F	1.44	0.031	1.44	0.022
2M:4F	1.47	0.034	1.46	0.024
2M:5F	1.50	0.038	1.52	0.028
3M:3F	1.49	0.045	1.51	0.031
3M:4F	1.54	0.045	1.55	0.031
3M:5F	1.58	0.049	1.62	0.036
Nested				
1M:3F	1.30	0.019	1.33	0.014
1M:4F	1.35	0.026	1.36	0.018
1M:5F	1.37	0.029	1.37	0.020
1M:6F	1.39	0.034	1.40	0.024
1M:7F	1.40	0.035	1.41	0.026

The empirical estimates included selection index 2, and 50 and 10 individuals recorded for BW_I and BW_{IV}, respectively. Note that the differences in genetic gain between schemes with 200 and 300 tanks are only due by chance.

breeding programs of dairy cattle utilizing multiple ovulation and embryo transfer (MOET) (Woolliams, 1989). Due to the artificial increase in the fecundity of cows in MOET schemes, it is possible to mate dams to many sires in a single generation. Woolliams (1989) further show that the factorial designs in MOET schemes proved to increase the rates of genetic gain by 12%. This was a result of an increase in selection intensity rather than in the accuracy of estimated breeding values. Indeed, the accuracy appeared to be very similar between nested, factorial and single pair mating designs (Woolliams, 1989), which was consistent with the results of the present paper. For instance, in our study the accuracy differed only marginally among the nested designs and factorial designs utilizing full resources (Fig. 4). Another advantage of using designs other than nested is that when common environmental effects influence the expression of traits, factorial

designs provide more accurate estimates of the breeding values compared to nested designs (Berg and Henryon, 1998), and hence lead to higher genetic gains. In fish
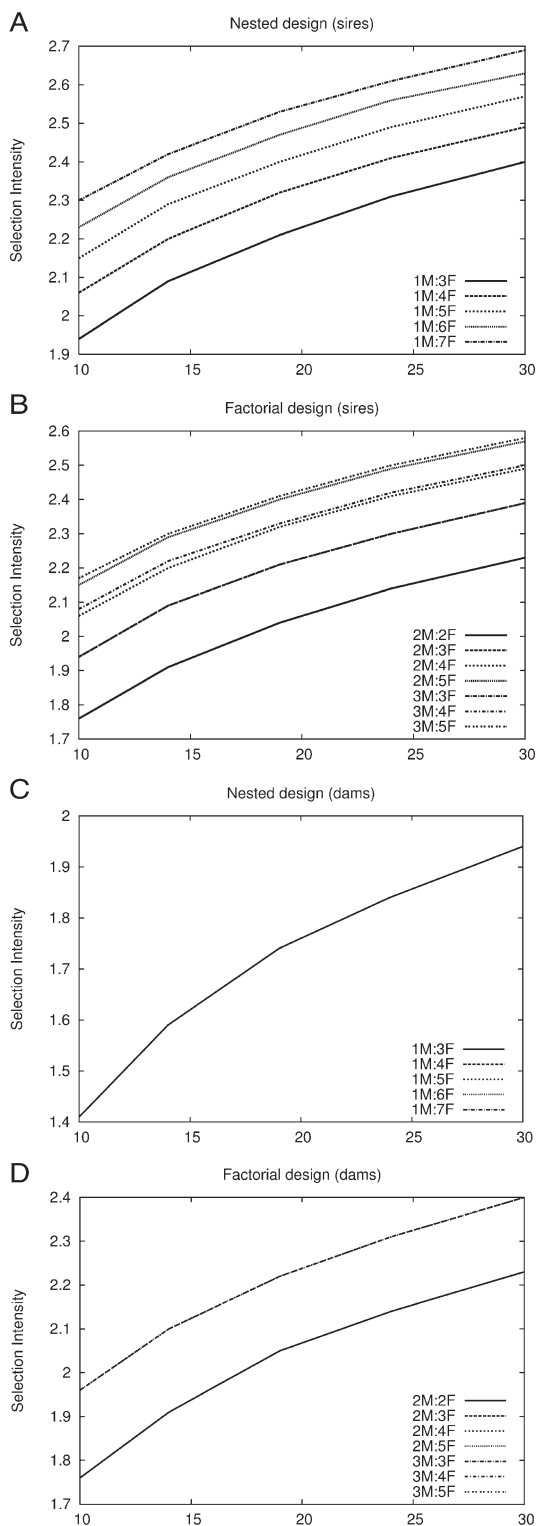
Fig. 3. Selection intensity as a function of number of breeding candidates per family survived to spawning. Intensity is given separately for sires in nested (A) and factorial mating designs (C), and for dams in nested (B) and factorial designs (D). Different mating ratios (M:F) are indicated by distinctly marked lines. Note that in nested designs selection intensities of dams are the same irrespective of the mating ratio used (B). In factorial designs selection intensity of dams differs only when either 2 or 3 males are mated to a variable number of females in the set (D).
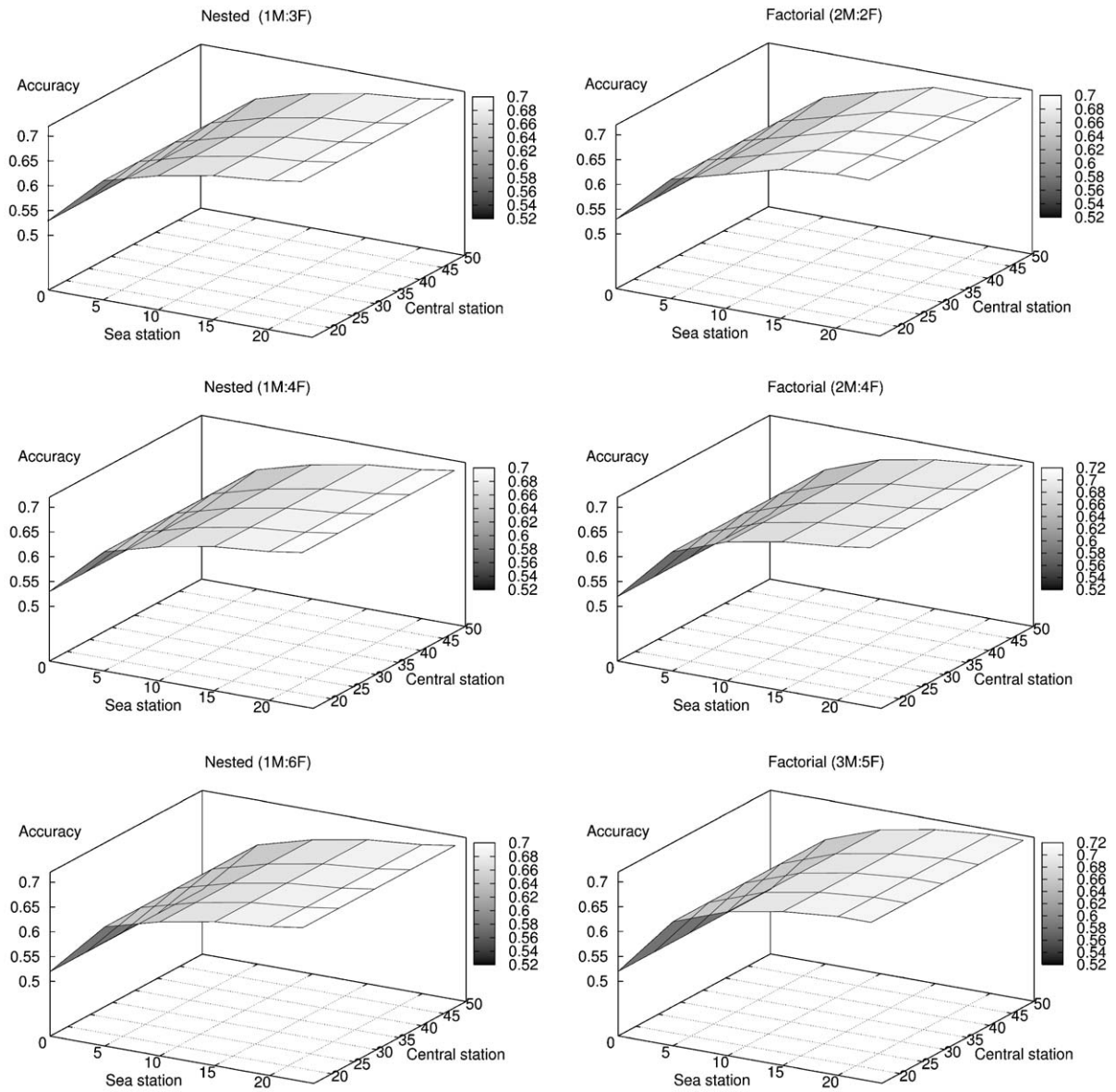
Fig. 4. Accuracy of breeding values as a function of number of individuals per family recorded for BW_I at the central and BW_{IV} at the sea station. Nested and factorial mating designs with different male to female mating ratios (M:F) are shown. Selection index Ig(2) was used in all cases.

breeding programs, common environment effects arise, for example, when full sibs are held in a common tank during the early stages of growth (Martinez et al., 1999). In paternal nested designs common environmental effects are confounded with the genetic effects of the dams, and thus, estimates of the breeding values of full-sib progeny (and therefore the breeding values of dams) are biased. For the same reason, genetic parameters are estimated with high precision using factorial designs in the presence of tanks effects (Berg and Henryon, 1998).

An increase in the number of individuals recorded per full-sib family at the central station lead to an increase in the genetic gain of the breeding objective. This was mainly due to an increase in selection intensity. The accuracy was improved notably by increasing the number of relatives measured at the sea station, but not when the number of relatives at the central station was increased. From a practical point of view the results shed lights upon the number of traits needed to be measured when a specific breeding objective is considered. The change of an index that incorporates more body weight traits expressed at the central station (for example, Ig(3) vs. Ig(2)) did not increase the genetic gain. This was due to the fact that including BW_{III} in the index gave little

extra information to predict BW_{IV}, because of the high genetic correlation of BW_{III} with BW_{II} and the lower genetic correlation of BW_{III} with BW_{IV}. By understanding which traits do and which do not provide extra information for predicting the breeding values, efforts of record keeping within breeding programs can be diverted to obtain information from other traits, such as those related to carcass quality or maturation. An appropriate profit analysis would be required to include these traits in a more complex breeding objective.

4.2. Rates of inbreeding in alternative breeding designs

Our empirical results showed that the rates of inbreeding were generally higher in the present study for factorial mating designs than for nested designs (Table 4). This is in contrast with the previous results showing that factorial mating designs can be used to increase the effective population size under selection (Woolliams, 1989; Engstron et al., 1994). The most likely explanation for this inconsistency is that in the present study, the number of full-sib families, and concomitantly the family size was fixed in all the designs due to restricted rearing facilities, which is a realistic scenario under practical conditions. Full-sib families have to be held in isolated family tanks to maintain the individuals' pedigree information. This is a major difference to the MOET schemes realized in dairy cattle in which factorial designs are carried out to decrease the actual size of full-sib progeny (see Woolliams (1989) for an example of an implementation). Since the rates of inbreeding under selection are due to the probabilities of co-selection of relatives, there is a greater chance of selecting related full sibs when factorial designs are implemented. This situation is particularly extreme in this example because most of the information in the breeding objective is obtained from relatives and not from candidates themselves. For this reason, there is more weight on the family mean rather than on individuals' information, and therefore, the chance of selecting individuals from a few families is high.

The rates of inbreeding ranged from 2% to 5% in the breeding designs with 200 tanks analyzed in the present paper (Table 4), which are slightly higher than those found in the selected populations of rainbow trout in Norway and Finland (Pante et al., 1998, 2001; Kause et al., 2005). However, these values are not comparable because our estimates do not account for the effect of non-random mating on ΔF. Non-random mating is practiced in the fore mentioned breeding programs. Pante et al. (1998) mentioned that keeping track of

pedigree data and avoiding full or half-sib mating could be sufficient to obtain tolerable rates of inbreeding in selected populations. However, this practice is only effective in the short term. More comprehensive methods have been developed using the theory of the optimal genetic contributions (Wray and Goddard, 1994; Meuwissen, 1998; Grundy et al., 1998). Using optimal genetic contributions, inbreeding can be restricted by dynamically minimizing the co-ancestry between selected individuals while maximizing the rate of genetic gain in the long term (Meuwissen, 1998). Such method is currently used in the Finnish breeding program for rainbow trout (Kause et al., 2005).

One measure of a risk of a breeding program is coefficient of variation of response (CVR), which can be approximated following Nicholas (1989) as:

$$CVR = \frac{2L^{1/2}}{\Delta G(N_e t)^{1/2}} \tag{8}$$

where L is a generation interval, and t is a time horizon that a breeder is willing to operate (arbitrarily assigned here to be 20 years or ≈ 6 generations of the Finnish breeding program), N_e is effective population size under selection (obtained from Table 4) and ΔG is rate of genetic gain per generation. The evaluation of this approximation leads to the values of about 12% in all the breeding programs studied here. These values are within the guidelines of acceptable risk that a breeder may be willing to accept in short to medium term (Nicholas, 1989).

As pointed out by Hill (1986), any discussion about the rates of inbreeding in breeding programs must consider the time horizon in which a breeder is expected to operate. If a population is to be bred only for a few years, it is clear that a breeder should select as intensively as possible and not to be concerned with either maintenance of genetic variation or inbreeding depression. As the time horizon increases, the loss of genetic variation and inbreeding depression are likely to play a key role in determining the long term rate of genetic gain (Hill, 1986), and thus, the rate of inbreeding has to be taken into account. However, there is no general solution how to find a balance between short and long-term selection responses; the conclusions depend on momentary discounts rates, risks of financial failure, and predictions of market share (Hill, 1999).

5. Conclusions

The present paper has shown that changes in the rates of genetic improvement can be accrued by changing the

structure of a breeding population. The modifications are simple and therefore the practical implementation of these changes is relatively straightforward. Nevertheless, this study highlights that more research is needed to find optimal breeding programs that incorporate a posteriori methods to constrain the rates of inbreeding while still maintaining high rates of genetic gain.

Acknowledgements

Appendix A

Outline of the breeding cycle of the Finnish breeding program in rainbow trout.

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