UNIVERSIDADE ESTADUAL PAULISTA
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CÂMPUS DE JABOTICABAL

MATE SELECTION IN AQUACULTURE SPECIES

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2018

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Thesis presented to the Faculdade de Ciências Agrárias e Veterinárias – Unesp, Campus of Jaboticabal in partial fulfilment of requeriments for the degree of doctor in Genetics and Animal Breeding.

2018

Yoshida, Grazyella Massako
Y54m Mate selection in aquaculture species / Grazyella Massako Yoshida. – – Jaboticabal, 2018
xii, 72 p. : il. ; 29 cm

Tese (doutorado) - Universidade Estadual Paulista, Faculdade de Ciências Agrárias e Veterinárias, 2018
Orientador: Roberto Carvalheiro
Coorientador: Sandra Aidar de Queiroz
Coorientador: José Manuel Yáñez
Banca examinadora: Carlos Antonio Lopes de Oliveira, Humberto Tonhati, Rafael Vilhena Reis Neto, Danísio Prado Munari
Bibliografia

1. Ganho genético. 2. Endogamia. 3. Variabilidade genética. 4. *Oncorhynchus kisutch.* 5. *Oreochromis niloticus.* 6. Dados simulados. I. Título. II. Jaboticabal-Faculdade de Ciências Agrárias e Veterinárias.

CDU 639.3.03

Ficha catalográfica elaborada pela Seção Técnica de Aquisição e Tratamento da Informação – Diretoria Técnica de Biblioteca e Documentação - UNESP, Câmpus de Jaboticabal.

UNIVERSIDADE ESTADUAL PAULISTA

Câmpus de Jaboticabal

CERTIFICADO DE APROVAÇÃO

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Jaboticabal, 26 de fevereiro de 2018

AUTHOR'S CURRICULAR DATA

GRAZYELLA MASSAKO YOSHIDA - born on June 19th, 1987 in Maringá - PR, daughter of Luiz Siro Yoshida and Neusa Y. Yaguinuma Yoshida. Started the university study in Animal Science at *Universidade Estadual de Maringá* in March 2005 and concluded in January 2012. During the undergraduate was granted with a scientific/technological initiation scholarship from the "*Conselho Nacional de Desenvolvimento Científico e Tecnológico - CNPq*" for two years to study Nile tilapia breeding under supervision of Prof. Ph.D. Ricardo Pereira Ribeiro. Started the M.Sc. course in Animal Science at the same University in February 2012 and concluded in February 2014. Was granted with a scholarship from "*Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq*" and presented her master with the dissertation entitled "*Avaliação genética e de efeitos ambientais em características reprodutivas de tilápia do Nilo***"** with Prof. Ph.D. Eliane Gasparino as advisor. Started the Ph.D. course in Genetics and Animal Breeding at *Universidade Estadual Paulista "Julio de Mesquita Filho" – FCAV/UNESP* – Campus of Jaboticabal in March 2014. Was granted with a scholarship from "*Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - CAPES*" and later on was granted with scholarship from "*Fundação de Amparo à Pesquisa do Estado de São Paulo – FAPESP*". During the doctorate's course, held an intership at *Universidad de Chile*, under supervision of Prof. Ph.D. José Manuel Yáñez, with a scholarship from FAPESP and a project entitled "*Selección de apareamiento en salmón coho*". Submitted to the final exam to obtain the Doctorate's degree in Genetics and Animal Breeding on February 26th 2018, with the thesis entitled "Mate selection in aquaculture species", with Ph.D. Roberto Carvalheiro as advisor.

"What is success?

To laugh often and much; to win the respect of intelligent people and the affection of children; to ear the appreciation of honest critics and endure the betrayal of false friends; to appreciate the beauty; to find the best in others; to leave the world a bit better…. to know even one life has breathed easier because you have lived.

This is to have succeeded!"

(Ralph Waldo Emerson)

I dedicate this thesis to my father, Luiz Siro Yoshida (in memoriam),
for earning an honest living for us
and to teach me always to "do the right thing".

I offer this thesis to my mother, Neusa Yoshida,
a strong and gentle person, that always believe in me and
encouraging me to always go further.

ACKNOWLEDGEMENTS

Firstly, I would like to thank God without whom nothing is possible.

My appreciation goes to my advisor, Ph.D. Roberto Carvalheiro. I am extremely grateful for his meaningful assistance, tireless guidance and patience. Thank you for the extensive professional and personal advices, for believing in me and in my work.

I would like to thank my co-advisor, Prof. Ph.D. Sandra Aidar de Queiroz, for initially accepted me as her doctoral student and for the support during these years. To my co-advisor and abroad internship supervisor, Prof. Ph.D. José Manuel Yáñez, for the great opportunity and the experience of work with his research group, to rely in my work and for friendship. Muchas gracias!

Special thanks go to *Programa de Pós-Graduação em Genética e Melhoramento Animal* from *Faculdade de Ciências Agrárias e Veterinárias (*Campus of Jaboticabal) for the opportunity to be part of students group.

I am gratefully acknowledge to PeixeGen research group (Universidade Estadual de Maringá – Maringá, PR) and Aquainnovo S.A. (Puerto Montt, Chile) to provide the Nile tilapia and coho salmon dataset, respectively.

I would like to thank the *Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - CAPES* and the *Fundação de Amparo à Pesquisa do Estado de São Paulo - FAPESP* (Process n. 2014/20626-4 and 2015/25232-7) for the fellowships.

Me gustaría dar las gracias a la Faculdad de Ciencias Veterinarias y Pecuarias de la Universidad de Chile y especialmente al Grupo de investigación en *Aquaculture Genetics and Genomics Lab,* por recibirme tan bien durante mi pasantía. Agradezco a mis colegas desde Chile: Liane Bassini, Jean Paul Lhorente, Ana Jedlicki (Moni), Agustín Barria,

Pablo Dufflocq, Halley Rodríguez, M. Eugenia Dinamarca, Katharina Correa, René Figueroa y claro, la linda M. Isabel Yáñez, por toda la ayuda y apoyo durante el período que viví ahí. Muchas gracias Chiquillos, ustedes hacen falta!

I am grateful for the support from "*Salinha's"* colleagues: Giovana Vargas, Henrique Costa, Laiza Iung, Daiane Becker, Thaise Melo, Baltasar Neto, Helsí Isidro and Ángel Lázaro. I am also grateful to Natalí Kunita, Fernanda Tanamati, Milene Hata and Rafael Kuradomi for their friendship and company.

Finally, I am very grateful to my family, who have been so wonderfully supportive. You're the reason why I keep walking, I keep facing all the struggles, pains and hardships. Special thanks goes to Yubi (my baby dog), for always joining with me and for unconditional love.

"Gratitude is the memory of the heart."

(Antístenes)

Muito obrigada!

Muchas gracias!

Thank you!

SUMMARY

MATE SELECTION IN AQUACULTURE SPECIES

ABSTRACT – the aims of this work were: (i) test the efficiency of mate selection (MS) algorithm in controlling the inbreeding and coancestry level, as well, increase the genetic gain; (ii) include the genetic variability of the future progeny as component for the optimization of the MS objective function in two aquaculture real dataset; and (iii) compare MS among truncation selection (TS) and optimum contribution selection (OCS) scenarios combined to different mating strategies to assess the best method in controlling inbreeding and maintain the genetic gain, for aquaculture breeding using simulated dataset. For objective (i) and (ii), a total of 8,782 Nile tilapias (NT) from five generations and 79,144 coho salmon (CS) from eight generations were used to optimize the objective functions (OF) and twenty discrete generations were simulated for the objective (iii), considering 50 families and 2,000 offspring per generation, and a trait with heritability of 0.30. The OFs were optimized accounting to coancestry of parents, expected genetic merit and inbreeding of the future progeny for the objective (i) and (iii) and in addition the genetic variability of the future progeny was considered for the objective (ii). For the objective (i), the mate selection allowed reducing inbreeding up to 73% for NT, compared with truncation selection, and up to 20% for CS, compared with realized scenario. In the objective (ii), MS allowed producing animals with higher (SD = 0.77 and 0.30 for NT and CS, respectively) or lower (SD = 0.25 and 0.14 for NT and CS, respectively) dispersion of estimated breeding value, depending on the objective function optimized. For real data set the MS outperformed the real mates and truncation selection and in addition the genetic variability of the future progeny could be changed when this component was considered in the OF. For the simulated dataset, the MS outperformed the TS and OCS followed by random mating. In the short-term, MS was more efficient than OCS + inbreeding minimizing in controlling inbreeding under the same genetic gain. However, in the long-term, OCS and MS resulted in similar genetic progress and average inbreeding, under the same weight on coancestry. In general, the mate selection algorithm was efficient and flexible to optimize objective functions accounting for different components, under practical applications in aquaculture breeding.

Keywords: genetic gain, genetic variability, inbreeding, *Oncorhynchus kisutch, Oreochromis niloticus,* simulate data

SELEÇÃO DE ACASALAMENTOS EM ESPÉCIES AQUÍCOLAS

RESUMO – os objetivos deste trabalho foram: (i) testar a eficiência do algoritmo de seleção de acasalamento (MS) em controlar o nível de endogamia e coascendência, além de aumentar os ganhos genéticos; (ii) incluir a variabilidade genética da futura progênie como componente de otimização na função objetiva de seleção de acasalamento usando dados de dois programas de melhoramento aquícolas; e (iii) comparar a MS com a seleção truncada (TS) e contribuição genética ótima (OCS), combinados com diferentes estratégias de acasalamentos para controlar a endogamia e manter os mesmo níveis de ganhos genéticos. Para os objetivos (i) e (ii), o total de 8.782 tilápias do Nilo (NT) de cinco gerações e 79.144 salmões coho (CS) de oito gerações foram utilizados para otimizar as funções objetivos e vinte gerações discretas foram simuladas para o objetivo (iii), considerando 50 famílias e 2.000 filhos por geração, e uma característica com herdabilidade igual a 0.30. As OFs foram otimizadas considerando a coascendência média dos pais, o mérito genético esperado, a endogamia da futura progênie para os objetivos (i) e (iii) e a variabilidade genética da futura progênie foi adicionada na OF para o objetivo (ii). Para o objetivo (i), a MS permitiu reduzir a endogamia em até 73% para tilápia do Nilo, em comparação com a seleção truncada e até 20% para o salmão coho, em comparação com o cenário real de acasalamento. No objetivo dois, a MS permitiu produzir progênie com maior (DP = 0.77 e 0.30 para NT e CS, respectivamente) ou menor (DP = 0.25 e 0.14 para NT e CS, respectivamente) dispersão dos valores genéticos, dependendo da função objetivo otimizada. A seleção de acasalamentos superou a seleção truncada e o cenário real de acasalamento e também foi possível alterar a variabilidade genética da futura progênie, quando esse componente foi considerado na OF utilizado os dados reais. Para os dados simulados, a MS teve melhor performance comparada com a TS e a OCS combinada com acasalamentos aleatórios. A curto-prazo, a MS foi mais eficiente do que a OCS combinada com os acasalamentos que minimizam a endogamia em controlar a endogamia sob o mesmo nível de ganho genético. Porém, a longo prazo os resultados entre as duas estratégias foram muito semelhantes. De forma geral, o algoritmo de seleção de acasalamentos foi eficiente e flexível em otimizar a função objetiva usando diferentes componentes, em diferentes aplicações práticas na aquicultura.

Palavras-chave: dados simulados, endogamia, ganho genético, *Oncorhynchus kisutch*, *Oreochromis niloticus*, variabilidade genética

CHAPTER 1 – General considerations

1.1 Introduction

Aquaculture has been responsible for the impressive growth in the supply of fish for human consumption with a production of 73.8 million tons in 2014 (FAO, 2016). The world population growth, rising living standards in developing countries and increased knowledge of the nutritional benefits of fish consumption for human health have contributed to the advancement of aquaculture (FAO, 2012).

In recent years, fish consumption has reached historical levels, with preliminary estimates for 2015 indicating an average global consumption over 20 kg/person/year (FAO, 2016). In terms of food supply, aquaculture made more fish available for consumption compared to capture production in 2014 (FAO, 2016). In the period from 2000 to 2012, the average annual increase in aquaculture fish production was 6.2% (FAO, 2014). From this scenario, it is estimated that by the year 2020 the fish, crustaceans and molluscs production will be 132 million tons and 43 million tons of seaweed (GJEDREM, 2012).

It is estimated that in 2025, freshwater species (carp, catfish and tilapia) will account for 60% of total aquaculture production (FAO, 2016). Tilapia is the second most produced freshwater species in the world. In 2015 the tilapia world production was 5.6 million tons (FITZSIMMONS, 2016). In Brazil, tilapia is the most produced species with 219.33 thousand tons in 2015, representing 45.4% of the total national production and an increase of 9.7% in relation to the year 2014 (IBGE, 2015).

The share of salmon and trout in world trade has increased strongly in recent decades, becoming the largest single commodity by value in 2013 and is also projected to continue to grow in the next decade. The farmed salmon industry has grown substantially in the past 40 years and today approximately 60% of the world's salmon production is farmed. In 2015 more than 2,200,000 tons of farmed salmon were produced, against around 880,000 tons of wild salmon which were caught (MARINE HARVEST, 2016). Chile is the largest producer of coho salmon (*Oncorhynchus kisutch*) globally,

reaching about 160,000 tons in 2014, representing more than 90% of total production (FAO, 2016).

According to Gjedrem et al. (2012) consumption of fish, molluscs and crustaceans will increase to 25.2 kg per capita by the year 2020. Considering the scenario where 50% or more of the world aquaculture production comes from improved stocks (higher growth rate, better feed conversion, resistance to disease), the overall aquaculture production will increase faster as the use of genetically improved stock.

The firsts aquaculture breeding programs were started in the early 1970s for Atlantic salmon (*Salmo salar*) and rainbow trout (*Oncorhynchus mykiss*) and several efficient breeding programs have also been started in the 1990s for other species including tilapia and shrimp (GJEDREM; BARANSKI, 2009; GJEDREM, 2012). Although the selection response is usually higher in fish and shellfish than in farm animals (OLESEN et al., 2003), aquaculture selection programs are not commonly used by the industry and the production of many species still relies completely on catching wild broodstock. Only less than 10% of the world's aquaculture production is based on genetically improved stocks (GJEDREM, 2012).

Individual selection was the first selection scheme used in aquaculture breeding. It is easy to perform, does not require individual identification or maintenance pedigree records and it was for many years the most commonly used method of selection for aquatic species (GJEDREM; BARANSKI, 2009; GJEDREM; ROBINSON, 2014). However, the very high fertility of fishes and the high selection intensity applied on individual selection, can contribute to the high accumulated inbreeding effects resulting in depression of fitness and the unsuccessful of some breeding programs (MOAV; WOHLFARTH, 1976; HULATA et al., 1986; TEICHERT-CODDINGTON; SMITHERMAN, 1988; HUANG; LIAO, 1990).

Currently, the best linear unbiased prediction (BLUP; HENDERSON, 1984) is frequently used for aquatic species as a selection alternative based on breeding value (GJEDREM; BARANSKI, 2009). Considered one of the preferred methods for the prediction of breeding values, the approach uses all available information on relatives to estimate breeding values, while correcting for fixed, non-genetic effects and genetic

trends in the population (KENNEDY, 1990). The drawback of BLUP is that the high accuracy of breeding value estimation also promotes the chance of selecting multiple members of the same family or if truncation selection on estimated breeding values is practiced, it will result, in both cases, in greater genetic gain but also higher rate of inbreeding (NGUYEN; PONZONI, 2006; KESTEMONT et al., 2015).

Controlling inbreeding rates is important to secure long term genetic response to selection. It can be monitored maintaining full pedigree information and through combined between and within family selection (selection of limited individuals from each family or having representatives of as many family as possible in future generations). Moreover, several mating strategies or more effective approaches can be applied, as optimum contribution selection (OCS – WOOLLIAMS; THOMPSON, 1994; MEUWISSEN, 1997) and mate selection (MS - KINGHORN et al., 1999; KINGHORN; SHEPHERD, 1999).

1.2 Literature review

1.2.1 Inbreeding

Genetic improvement programs have been successfully carried out in Nile tilapia (BENTSEN et al., 2012) and in salmonids (GJEDREM, 2012, 2000) for increasing the productivity of economically important traits, mainly for growth traits and resistance against diseases. However, one of negative consequences of selective breeding may be the accumulation on inbreeding (ROBERTSON et al., 1961). In fish and shellfish species, the problem on inbreeding is even greater. Due to the very high fecundity, the risk of rapidly building up inbreeding is very high, because only a few parents are needed to reproduce in each generation (GJEDREM, 2005).

The inbreeding increases in a population, results in the decreases of genetic variance, and the animals will become more similar phenotypically (GJEDREM; BARANSKI, 2009). This may put at risk a breeding scheme because it could reduce the additive genetic variance, and will reduce both heritability as well as genetic gain in a breeding program (FALCONER; MACKAY, 1996). Another detrimental effect of inbreeding is that the increase in homozygosity tends to ‘uncover’ undesirable recessive

genes, which may be lethal or semi-lethal (GJEDREM; BARANSKI, 2009). The most of deleterious or disease conditions are recessive, and are therefore more likely to be expressed in inbred populations. So, the inbreeding populations suffer from a reduction in fitness (GJEDREM, 2005).

The general reduction in performance due to inbreeding is known as inbreeding depression and the negative effect is most apparent in fitness traits like survival and reproduction, and for growth rate. Some authors have reported inbreeding depression affecting quantitative traits in fish. Aulstad et al. (1972) and Kincaid, (1976) found that inbreeding causes an increase in rainbow trout post larvae deformity, decrease the feed conversion efficiency, and body weight during the first year of the animal life. In Nile tilapia, increased inbreeding rates are related to reduce in the fecundity (FESSEHAYE et al., 2009), the weight at tagging and a lower survival rate (FESSEHAYE et al., 2007). In a coho salmon population, the selection for growth rate and survival was performed over nine and ten generation for even and odd population, respectively, and the inbreeding coefficient were estimated to be over 22% (MYERS et al., 2001). Yáñez et al. (2014) emphasized the need to use strategies to constrain the inbreeding levels in a Chilean coho salmon population.

Strategies to control the rate of inbreeding may include the selection of more parents per generation, increase the number of selected animals per family, introduce unrelated individuals as parent in selection program, and choice of mating design (GJEDREM; BARANSKI, 2009; WOOLLIAMS, 1989). However, in a practical situation such procedures may have not be viable. For instance, the number of parents selected cannot be increased unless more tanks are made available. Increase the number of selected animals per family results in more cost to tagging and labor cost, while introducing wild genetic material could affect the genetic progress (GJEDREM; BARANSKI, 2009). Therefore, mate allocation strategies for containing inbreeding levels in aquaculture species (PONZONI et al., 2010) using optimal contributions selection (WOOLLIAMS; THOMPSON, 1994; MEUWISSEN, 1997) or mate selection (KINGHORN et al., 1999; KINGHORN; SHEPHERD, 1999) are recommend to better control the inbreeding levels, and will be describe below.

1.2.2 Optimum contribution selection

Optimum contribution selection (OCS) maximizes genetic response while constraining inbreeding by restricting the coancestry among selected parents (WRAY; GODDARD, 1994; MEUWISSEN, 1997; MEUWISSEN; SONESSON, 1998; GRUNDY et al., 1998; GRUNDY et al., 2000). Maximizing long-term genetic gain, reducing the risks of inbreeding, genetic drift and undesirable changes in gene frequencies are the benefits of OCS.

The method uses an index (objective function; OF) to assess the potential contribution accounting for the magnitude of the BLUP-EBV (estimated breeding value) of a candidate and its relationship with the other selection candidates. An ideal individual to select is an animal with high breeding value, but that is little related to the other selection candidates (GJEDREM, 2005). The OCS usually considered the expected merit of the future progeny and coancestry among selected parents as components for the objective function to be optimized.

After the candidates to reproduction are selected using OCS, the next step is to define the mates. This can improve the genetic structure of the population for the next round of selection. Some studies have been carried out assuming random mating among selected parents utilizing OCS (MEUWISSEN, 1997; GRUNDY et al., 1998; MEUWISSEN; SONESSON, 1998; GRUNDY et al., 2000). On the other hand, several systematic mating criteria can be used for generating less inbreeding while producing at least as much genetic gain as random mating, such as minimum-coancestry, compensatory, non-random and minimum-variance mating (CABALLERO et al., 1996).

The OCS is a flexible approach and have been used in practical animal breeding programs as, for example, in UK Holstein dairy cattle population (KEARNEY et al. 2004), in British livestock populations of sheep and beef cattle (AVENDAÑO et al. 2003) and in a large salmon fish breeding stock (HINRICHS et al. 2006). According to Meuwissen (1997), the OCS method has outperformed standard truncation BLUP selection at the same predefined rate of inbreeding and improved the long-term response to selection by 21 to 60%.

In aquaculture species, OCS has been shown to be effective in optimizing genetic gain under controlled level of inbreeding (SONESSON, 2005; HINRICHS et al., 2006; D'AGARO et al., 2007; HOLTSMARK et al. 2008a and b). Skaarud et al. (2011) shown that OC can be applied in a practical way to control inbreeding in fish breeding programs, with better or equal results as the commonly used method, which implies a fixed quota of breeders from each family.

1.2.3 Mate selection

Selective breeding schemes for animal generally involve two steps. The selection step determines the increase in average coancestry of the population, as a consequence of selecting related superior animals, and the mating step can improve the genetic gain of the population for the next round of selection (SONESSON; MEUWISSEN, 2002). Selection step is the largest impact on the aim of most breeding schemes, mainly to maximize genetic gain while maintaining inbreeding at, or under, pre-defined levels. On the other hand, developing and implementing mating criteria appropriately can further improve genetic gain and/or reduce inbreeding, it is can be an additional benefits to a breeding scheme without extra costs or practical constraints (HENRYON et al., 2009). Furthermore, as suggested by Fernández & Toro (1999) optimizing mating schemes can be computationally intensive, makes it unpractical for large population. The solution can be optimize selection and mating in two separate steps (OCS), so only the selected animals have to be considered, although this method may not result in maximum genetic response because all possible mating of selection candidates are not considered (SONESSON; MEUWISSEN, 2000).

In mate selection, decisions on who to select for breeding and how mates should be allocated are simultaneously considered in one-step approach (SHEPHERD; KINGHORN, 1999). Mate selection was carried in order to optimize an objective function containing different components, like predicted genetic merit of progeny, long-term inbreeding as reflected by parental coancestry, progeny inbreeding, heterosis and various costs and logistical constraints associated with the breeding program (SHEPHERD; KINGHORN, 1999; BANKS, 2000; KINGHORN, 2000; KINGHORN et al., 2008;

CARVALHEIRO et al., 2009). The objective function can be changed (variables added or deleted) to suit the desired outcomes of the breeder if constraints arise (NEWMAN, et al., 2010).

Selection and mating decisions can be represented by a decision matrix *X* with elements *Xij* indicating whether male *i* is mated (*Xij = 1*), or not mated (*Xij = 0*), to female *j*. For each mating set tested, the component outcomes evaluated constitute the overall Mate Selection Index (MSI). The computing challenge is to find the mating set that gives the best MSI. For this purpose, an evolutionary algorithm was developed by KINGHORN (1998), based on Differential Evolution (PRICE; STORN, 1997). The set of matings shown is an hypothetical test mating set (Figure 1). The mating set is evaluated for all components in the MSI. An efficient algorithm for finding the best mating set is required.

The mate selection driver shown in Figure 2 was developed to conduct the search across all legal mating sets. The underlined figures drive the three matings noted, and these are the values to be optimised. “No. of uses” (second column for males, second row for females) is the number of matings for which each animal should be used, and this in turn drives selection, including extent of use of each animal. An animal is culled if this is set to zero. “Ranking criterion” is simply a real number. It is ranked to give the column “Rank”. This in turn drives the mate allocation. The first ranked male mating is the single mating from male 3. He is thus allocated to the first available female mating (one mating from female 1). The second ranked male mating is the first mating from male 1 and he is thus allocated to the second available female mating (the one mating from female 3). The third ranked male mating is the second mating from male 1 and he is thus allocated to the third available female mating (the one mating from female 4).

Studies investigating the mate selection algorithms were carried out by Kinghorn & Shepherd (1999b), Sheperd & Kinghorn (1999), and Kinghorn (2011) it was possible the implementation of this methodology in breeding programs. In studies using real cattle data, Weigel & Lin (2000) and Carvalheiro et al. (2009; 2010a), demonstrated the importance of the use of computer programs in the selection of breeders for reducing inbreeding and increasing genetic gains. In management of conservation programs, mate selection was more efficient than using the two-step selection strategy, preserving genetic

diversity more effectively and maintaining the fitness of the population (FERNÁNDEZ et al., 2001). In aquaculture species, the application of mate selection is being reported for the first time in this work.

1.2.4 Differential evolution algorithm

Mate selection represents a flexible strategy either to improve genetic progress or to reduce inbreeding and it can be solved using different algorithm (DE – STORN; PRICE, 1995). This is an efficient and robust optimization algorithm for agricultural models. The DE is a stochastic direct search technique, based on the mechanisms of natural evolution of the species, using procedures of selection, organized based on the adaptive value of the individuals and operators of mutation and recombination (STORN; PRICE, 1997).

The concept of DE, according to Mayer, (2005), start with a initial population (P) of candidate members (each being a string of ‘genes’, one per management option for the model) is established, usually at random. Each population member is characterized by its fitness. For each population member in turn, a challenger is constructed. If this challenger has superior fitness, it will replace the population member in the next generation. To construct this challenger, three other population members are chosen at random. We can label these as *a*, *b* and *c*. Each gene (management option, as coded on to DE’s alleles) is then addressed in turn. With a probability equal to the crossover rate (CR), the gene is simply adopted from the population member that the challenger is challenging. Otherwise, a new gene value is constructed as the value for member *a* plus the mutation factor (F) times the difference between the values for *b* and *c*. Successful challengers replace their respective population members and, together with surviving members, constitute a new generation with higher mean fitness. The process continues over sufficient generations to achieve convergence close to an optimal solution, with the fittest solution being chosen.

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CHAPTER 2 - Mate selection in aquaculture breeding using differential evolution algorithm

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Published in Aquaculture Research (Online ISSN: 1365-2109) - DOI: 10.1111/are.13365

Abstract - An algorithm to perform mate selection in aquaculture breeding using a simple computational optimization procedure called "differential evolution" (DE) was applied under optimum contribution selection and mate selection scenarios, to assess its efficiency in maximizing the genetic merit while controlling inbreeding. Reals aquaculture datasets with 8,782 Nile tilapias from five generations and 79,144 coho salmon from eight generations were used to optimize objective functions accounting for coancestry of parents and expected genetic merit and inbreeding of the future progeny. The mate selection results were compared with those from the realized scenario (real mates), truncation selection and optimum contribution selection method. Mate selection allowed reducing inbreeding up to 73% for Nile tilapia, compared with truncation selection, and up to 20% for coho salmon, compared with realized scenario. There was evidence that mate selection outperformed optimum contribution selection followed by minimum inbreeding mating in controlling inbreeding under the same expected genetic gain. The developed algorithm was computationally efficient in maximizing the objective functions and flexible for practical application in aquaculture breeding.

Keywords: coancestry, evolutionary algorithms, inbreeding, optimum contribution, *Oncorhynchus kisutch, Oreochromis niloticus*

2.1 Introduction

At nucleus level the main goal of aquaculture breeding programs is to maximize the genetic gain for a specific trait or a combination of traits, which needs to be coupled with some strategy to control inbreeding for avoiding inbreeding depression and for maintaining genetic variability and selection response in the long-term. Inbreeding is a critical issue in breeding programs, especially for aquaculture species which usually present high fecundity capacity allowing high selection intensities and, as a consequence, a small number of parents may produce all the progeny of each generation. The reduced number of families poses a challenge to control inbreeding rate.

Different strategies and methods have been proposed to control inbreeding rate in breeding programs, as the optimum contribution (OC) selection (Woolliams & Thompson, 1994; Meuwissen, 1997) that aims to maximize the genetic level under constrained rate of inbreeding. In OC selection, the intensity of use of each selection candidate is optimized according to an index that basically contains the expected genetic merit of the future progeny and the coancestry among selected parents. Several studies have shown the benefits of implementing OC in aquaculture breeding programs, in terms of maximizing genetic response with controlled rate of inbreeding (Kause et al.; 2005; Sonesson, 2005; Hinrichs et al.; 2006; Holtsmark et al.; 2008; D'Agaro et al.; 2010; Nielsen et al.; 2011; Skaarud et al.; 2011; 2014; Liu et al.; 2015).

Another alternative to control inbreeding is the mate selection (MS) strategy (Kinghorn et al.; 1999; Kinghorn & Shepherd, 1999). In MS, selection and mating decisions are performed simultaneously. This single step approach is suitable to accommodate different key issues faced by animal breeders and to find a global optimum solution (Kinghorn, 2011). To implement MS an objective function (OF) needs to be defined and maximized. For instance, Kinghorn et al. (1999) applied MS using an OF accounting for expected merit and inbreeding of the future progeny and coancestry among selected parents. In this case, inbreeding of the future progeny would also drive selection besides defining the mates, what is expected to be advantageous since the best animals to be selected can be dependent on the allocation of the mates and vice versa (Kinghorn et al.; 1999). Studies conducted by Kinghorn & Shepherd (1999), Sheperd & Kinghorn

(1999), Weigel & Lin (2000), Fernández et al. (2001), Carvalheiro et al. (2009; 2010), Kremer et al. (2010) and Kinghorn (2011) showed that MS is effective in controlling inbreeding and maximizing genetic gain. To our knowledge, no study has investigated the use of MS in aquaculture breeding programs. Furthermore, it is not clear in the literature if there is advantage of using MS in comparison with OC selection.

This study was carried out aiming to apply MS in aquaculture breeding, in real datasets under different scenarios, to assess its efficiency in maximizing the genetic merit while controlling inbreeding, as well as compare MS against truncation and OC selection strategies.

2.2 Material and Methods

2.2.1 Nile tilapia dataset

PeixeGen Research Group from Universidade Estadual de Maringá, Maringá, PR, Brazil provided the Nile tilapia (*Oreochromis niloticus*) dataset used in this study. The PeixeGen Research Group run a breeding program established in 2005 with the importation of 600 animals (~30 families) from Malaysia.

The dataset contained pedigree information and standardized estimated breeding values (sEBV) for harvest weight of 8,782 Nile tilapias from five generations. The numbers of sires and dams per generation are presented in Table 1.

The animals evaluated in each generation were obtained from a hierarchical mating design (two dams per sire), producing full and half-sib families. The families were produced through natural mating in separate breeding hapas (1 m^3 volume) at the Fish Farming Experimental Station of Universidade Estadual de Maringa (UEM - CODAPAR), district of Floriano, Maringa, PR, Brazil. Inspection of the presence of spawning was done two times per week, when the sire was removed and placed together with another dam in a different hapa. The larvae were kept with their dams until the end of the breeding season (up to 3 months). This common environment effect was adjusted to calculate the EBVs.

At the end of the reproduction period, 100 fingerlings from each family were divided into two equal groups, which were transferred to a nursery structure and kept in hapas of 1 m^3 in the earthen pond. When fingerlings reached 10 g, 50 animals of

each full-sib family were individually identified by Passive Integrated Transponder (PIT) tags, implanted in the visceral cavity.

Table 1. General information, inbreeding coefficient, standardized estimated breeding value and standard deviation for Nile tilapia dataset, per generation.

Gen	Number				Inbreeding			sEBV±SD
	Sires	Dams	Families	Progeny	Mean	Min.	Max.	
1	24	33	33	1,731	0	0	0	-0.01±1.11
2	40	57	58	1,717	0	0	0	0.07±0.55
3	52	79	79	2,695	0	0	0	0.39±0.71
4	39	44	50	1,127	0.00319	0	0.06300	0.83±1.01
5	29	42	51	1,455	0.00016	0	0.00800	0.97±1.28

sEBV, standardized estimated breeding value; SD, standard deviation; Gen, generation; Min, minimum; Max, Maximum; sEBV = EBV/83.036.

Shortly after tagging, the animals were transferred to the grow-out system in cages located in Diamante do Norte, PR, Brazil. The volume of each cage was 6 m^3 (2x2x1.5m) and the density of fish per cage was approximately 150 fishes/m^3. All grow-out cages presented almost the same number of individuals per family. The growing period was approximately equal to 7 months (from March until October). At harvest time, body weight and sex information were recorded on all fishes. EBVs for body weight were calculated using best linear unbiased predictions (BLUP) (Henderson, 1984), under an animal model, including larval and fingerling hapas as random common environment effects; sex, cage nested to year and age at harvest as fixed effects.

2.2.2 Coho salmon dataset

Aquainnovo S.A provided the coho salmon (*Oncorhynchus kisutch*) dataset of AquaChile Breeding Program in Chile. The breeding program was established in 1997 and 1998 with two independent populations (odd and even), managed in two-year reproductive cycle (Dufflocq et al.; 2016). The dataset used in this study contained

pedigree information and standardized economic index of 79,144 coho salmon from the even population, comprising eight generations (Table 2).

Table 2. General information, inbreeding coefficient, standardized economic index and standard deviation for coho salmon dataset, per generation.

Gen	Number				Inbreeding			sIndex±SD
	Sires	Dams	Families	Progeny	Mean	Min	Max	
1998	42	81	81	8,619	0.000	0.000	0.000	-0.05±0.23
2000	36	73	73	6,557	0.002	0.000	0.125	0.37±0.30
2002	59	114	114	9,120	0.025	0.000	0.125	0.63±0.38
2004	49	137	137	10,761	0.047	0.000	0.172	1.32±0.31
2006	37	102	102	10,523	0.062	0.016	0.203	1.65±0.37
2008	34	98	98	8,821	0.063	0.027	0.191	1.97±0.33
2010	45	110	110	8,798	0.070	0.035	0.126	2.37±0.28
2012	61	112	112	15,945	0.081	0.056	0.162	2.74±0.36

sIndex, standardized economic index; SD, standard deviation; Gen, generation; Min, minimum; Max, Maximum; sIndex = Index/6.79329.

The spawning was induced using hormone and all families were generated within one or two weeks for minimizing the effect of date of spawning in weight at harvest. A nested design with three to five females per male was adopted and an average of 103 families per year.

As described by Yáñez et al. (2014a), the eggs of each full-sib family were incubated separately, and at eyed stage 2,000 eggs of each selected family were moved to individual tanks (400 l each). Then, the progeny was individually identified using PIT tags, between November and December of each year when the fishes weight about 5 to 7 g. At this stage, the fishes were transferred to smoltification sites in fresh water conditions where each full-sib family was randomly stocked in equal numbers (60–80) into two or three rearing cages. Smoltification occurred naturally at eight months post-spawning and weight at harvest time (~3 kg) was recorded at 20–21 months of age. In the

latter generation, resistance against *Piscirickettsia salmonis* was included into the breeding goal. The phenotypes were measured on sibs of the selection candidates by means of a challenge test performed as described by Yáñez et al. (2013) and the trait was defined as day of death (Yáñez et al.; 2014b). The genetic evaluation was carried out using a bivariate animal model, including the contemporary group of sex:cage:year and age at harvest, and tank and weight at the end of test as fixed effects for weight at harvest and resistance to *P. salmonis*, respectively (Yáñez et al.; 2016). Thus the two-trait selection index included EBVs for weight at harvest and resistance to *P. salmonis* weighted according to their relatives economic values.

2.2.3 Objective function

The MS was defined with the optimization of the following objective function (OF):

$$OF = w_1 x' EBV + w_2 x' Ax + w_3 \bar{F}$$

where, x'EBV is the expected merit of the future progeny; x'Ax is the weighted mean coancestry of selected parents; $\bar{F}$ is the expected average inbreeding coefficient of the future progeny; w_1 to w_3 are the corresponding weighting factors and x is the vector to be optimized of genetic contributions for each candidate (the symbol ' denotes a transposed vector).

Although not explicitly described in the OF, the mate allocations were determined by $\bar{F}$, following the problem representation suggested by Gondro & Kinghorn (2008). In this representation, an auxiliary vector is used internally in the mate selection algorithm with the number of elements equal to the number of mates. Each element of the auxiliary vector is a real number used to indirectly determine the mates. These real numbers are ranked and the resultant rankings ultimately define the mates to be performed. As an illustrative example, suppose that five mates need to be performed and the optimized x vector determines the contribution of three candidate sires as 3, 0 and 2, respectively. Let's also suppose that the ranking of the five elements of the auxiliary vector are (in order) equal to 2nd, 5th, 1st, 4th and 3rd, which determines that the first candidate sire would be mated with the 2nd, 5th and 1st available dam, and the third candidate sire would be mated

with the 4th and 3rd available dam. More information about this mate representation and its reasoning can be obtained in Gondro & Kinghorn (2008).

The optimization of the OF assuming w_2 and w_3 equal to zero corresponds to truncation selection. In turn, the optimization of the OF ignoring $\overline{F}$ (w_3=0) corresponds to the application of OC selection. Using a relatively very low value for w_3 corresponds to the application of OC selection followed by mating minimizing inbreeding as, in this case, the value of OF would primary be determined by the expected merit and coancestry and secondary by $\overline{F}$, i.e. $\overline{F}$ would only drive mate and not selection.

2.2.4 Mate selection algorithm

A mate selection algorithm based on Differential Evolution (DE – Storn & Price, 1995) was developed in FORTRAN language, performing proper changes in a previous developed DE algorithm to perform OC selection (Carvalheiro et al.; 2010), which loosely mimics a biological process evolving towards an optimal solution.

The terms “generation”, “population”, “chromosome”, “loci”, “allele”, “mutation”, “crossover” and “fitness” will be used to help illustrate the MS method, and these should not be confused with similar terms used for the animal breeding application itself.

The DE algorithm applied consisted in randomly generating an initial population of possible solutions, composed by the number of mates for each candidate (the elements of vector x) and by the real numbers of the auxiliary vector which indirectly defines the mates. Each individual of the population is considered a chromosome with n loci, where n is the number of candidates for selection (order of vector x) plus the number of mates (order of the auxiliary vector). The alleles are either random values ranging from 0 to the maximum allowed number of mates for each candidate (vector x) or real values (auxiliary vector). The fitness of each individual, determined by the value of the OF described above, is calculated according to the value (allele) of each locus of vector x, and to the expected inbreeding of the future progeny resultant from the mates indirectly determined by the auxiliary vector. Once the initial population is established, several generations are simulated. In each generation, a challenger is constructed for each population member. If

this challenger has superior fitness, it will replace the population member in the next generation. To build this challenger, three other individuals are chosen at random. We can label these as A, B and C. Each allele is then addressed in turn. With a probability equal to the crossover rate, the allele is simply adopted from the population member that the challenger is challenging. Otherwise, a new allele value is constructed as the value for member A plus the mutation factor times the difference between the values for B and C. Successful challengers replace their respective population members and, together with surviving members, constitute a new generation with higher mean fitness. The process continues over enough generations to achieve convergence close to an optimal solution, with the fittest solution being chosen.

The operational parameters of the DE algorithm to optimize the OF where: population size = 2 times the number of candidates; crossover rate = 0.5; mutation factor = 0.2 (or 0.9 every 4 generations); and maximum number of generations of the evolutionary process (maxgen) = 1,000,000. Convergence was assumed when the range and the mean absolute deviation of the OF, considering all the possible solutions per generation, were lower than $1x10^{-6}$. The best solution from the maxgen generation was considered as the optimum solution when the convergence criterion was not attained.

The approach proposed by Lampinen & Zelinka (1999) was adopted to provide integer solutions for the number of mates per candidate. To increase computational efficiency, Colleau (2002) indirect approach was adopted to calculate coancestry, and linked lists (Knuth, 1975) were used for the storage and calculations involving sparse matrices. The mate selection algorithm is freely available for research purpose and can be obtained under request to the corresponding author.

2.2.5 Nile tilapia scenarios

For all scenarios in Nile tilapia, it was considered as selection and mate candidates the best four females (179 animals) and six males (281 animals) per family, excluding those with negative EBVs, from the 51 families of the fifth generation. The males were allowed to be mated with a maximum of four females. Each female was mated once, i.e. the contribution of each female was not optimized.

A total of 13 OF were tested for Nile tilapia, under 3 different scenarios (Table 3). In the first scenario (Parametric space explore), the expected merit, coancestry and inbreeding coefficient were optimized independently in OF1 to OF3, respectively, aiming to explore the parametric space of the different components of the OF. The scenario 2 (OF4 to OF11) corresponded to OC selection. Firstly, different relative weights for w_1 and w_2 were considered and $\overline{F}$ was ignored (OF4 to OF10). After defining proper set of values for w_1 and w_2, a relatively small weight for $\overline{F}$ was used, corresponding to the application of OC selection followed by minimum inbreeding mating (OF11). In scenario 3 (OF12 and OF13), MS method was applied using the same weights for merit and coancestry as in OF11, but defining the weight for inbreeding in a way that selection and mating were performed simultaneously.

2.2.6 Coho salmon scenarios

The real 2012 coho salmon progeny (8^{th} generation) was formed by the mate between 61 sires and 112 dams from the year 2010 (7^{th} generation). This was considered as the real scenario (realized mates) and it was compared to the result of the “phantom” progeny (resultant from the mates recommended by the algorithm) from three different scenarios, to check the efficiency of the mate selection algorithm in more than one dataset.

A total of 10 OF were tested for coho salmon, under 3 different scenarios (Table 4). For the scenario 1 (Maximize and minimize inbreeding), the sires, dams and their intensity of use, were kept equal to the real scenario. The selection was intentionally not optimized and just the mates were optimized, aiming to minimize (OF1) or maximize (OF2) inbreeding. In scenario 2 (Sire use optimization - OF3 to OF6), the sires and dams were kept the same as in the real scenario, but the 61 sires were allowed to be mated with zero to four dams. In scenario 3 (Alternative mates - OF7 to OF10), the dams were kept the same as in the real scenario. The candidate sires were the three best males per family from the year 2010, resulting in 330 candidate sires, which presented similar genetic merit as the 61 original candidates. This scenario provides more opportunity for the algorithm

to find alternative mates to optimize the objective function, compared to the previous scenarios.

2.3. Results

2.3.1 Nile tilapia

The results from the optimization of the different objective functions applied in Nile tilapia are presented in Table 3. OF1 represents truncation selection and provided the highest expected genetic merit of the future progeny (2.4982). Coancestry and inbreeding were not optimized in OF1, and its results were used as a reference for comparison with those from the other objective functions. In OF2 and OF3, coancestry and inbreeding were maximized, respectively, to explore their parametric space. Compared to OF1, coancestry was increased by 70.18% in OF2, and inbreeding was increased by 124.86% in OF3 (Table 3).

The results from scenario 2 (Table 3) correspond to OC selection. In the first seven objective functions from this scenario (OF4 to OF10), inbreeding was ignored and the weight for coancestry varied from -1 to -100. As more importance was given to coancestry (from OF4 to OF10), the number of selected sires increased and the expected genetic merit and coancestry decreased. For instance, compared to OF1, OF10 resulted in 51.67 more sires being selected (60 *vs* 91 sires) and a reduction of 26.61 and 58.72% on genetic merit and coancestry, respectively. The different OF differed not only on the number of selected sires but also on the contributions of the common selected sires. As an example, from the 60 sires selected by OF1, only 30 were in common with OF10. These common sires contributed for 89 mates in OF1 and 61 mates in OF10.

Compared to OF1, results from OF6 revealed that the weights used to optimize this objective function allowed a substantial reduction on coancestry (22.95%) with a small reduction in the genetic merit (2.42%). OF11 corresponded to the application of OC selection followed by minimum inbreeding mating. It provided the same result as OF6 for genetic merit and coancestry, but allowed a greater reduction on inbreeding (34.97% *vs* 15.28%).

Table 3. Genetic merit, coancestry and inbreeding results from the optimization of different objective functions in Nile tilapia.

OF	w_1	w_2	w_3	nSire	x'EBV	x'Ax	$\overline{F}$	dif_x'EBV	dif_x'Ax	dif_$\overline{F}$
Scenario 1: Parametric space explore										
1*	1	0	0	60	2.49816	0.03323	0.01685	0.00	0.00	0.00
2	0	1	0	60	1.98516	0.05655	0.02292	-20.54	70.18	36.00
3	0	0	1	135	1.84122	0.02286	0.03787	-26.30	-31.08	124.86
Scenario 2: Optimum contribution selection										
4	1	-1	0	60	2.49758	0.03249	0.01421	-0.02	-2.20	-16.00
5	1	-10	0	65	2.47618	0.02812	0.01384	-0.88	-15.36	-17.87
6	1	-20	0	71	2.43772	0.02560	0.01428	-2.42	-22.95	-15.28
7	1	-30	0	73	2.36095	0.02253	0.01516	-5.49	-32.19	-10.08
8	1	-40	0	79	2.29398	0.02067	0.01334	-8.17	-38.07	-20.85
9	1	-50	0	80	2.22541	0.01904	0.01038	-10.92	-42.70	-38.38
10	1	-100	0	91	1.83347	0.01372	0.01370	-26.61	-58.72	-18.73
11**	1	-20	-0.00001	71	2.43772	0.02560	0.01096	-2.42	-22.95	-34.97
Scenario 3: Mate selection										
12	1	-20	-0.01	70	2.43847	0.02564	0.00580	-2.39	-22.84	-65.56
13	1	-20	-1	71	2.43364	0.02542	0.00459	-2.58	-23.51	-72.75

OF, objective function; w_1, w_2 and w_3, weights for genetic merit, coancestry and inbreeding, respectively; nSire, number of selected sires; x'EBV, genetic merit; x'Ax, coancestry; $\overline{F}$, inbreeding; dif_x'EBV, difference of expected genetic merit in percentage; dif_x'Ax, difference of coancestry in percentage; dif_$\overline{F}$, difference of inbreeding in percentage.

dif_x'EBV, dif_x'Ax and dif_$\overline{F}$: are compared to the respective results from the OF1.

*Corresponding to a truncation selection.

**Corresponding to the application of optimum contribution selection followed by minimum inbreeding mating.

In scenario 3 (OF12 and OF13), selection and mating decisions were performed simultaneously (MS). The results from OF12 and OF13 (Table 3) showed that MS outperformed OC selection followed by minimum inbreeding mating (OF11) in controlling inbreeding, under similar levels of genetic merit and coancestry. Compared to OF1, the reduction in the expected inbreeding of the future progeny was equal to 65.56% for OF12 and 72.75% for OF13, whereas it was equal to 34.97% for OF11.

2.3.2 Coho salmon

The results of the different objective functions applied to coho salmon using the same sires and dams, and their intensity of use, as in the real scenario, showed the possibility to reduce inbreeding by 15.25% (OF1) or to increase inbreeding by 55.84% (OF2), depending on the allocation of the mates, determined by minimizing or maximizing inbreeding of the future progeny, respectively (Table 4).

When the 61 sires from the real scenario were allowed to be mated with zero to four dams (Scenario 2; Table 4), the maximum expected index of the future progeny was obtained with OF3. In this case, the top 28 sires would be mated with four dams each, and the remaining 33 sires would not be mated. It is important to emphasize that this strategy would not be recommended in practice otherwise inbreeding rate would rapidly increase. Results from scenario 2 (Table 4) also showed that, giving the same candidates as in the real scenario, it would be possible to reduce coancestry and inbreeding by 3.17% and 16.24%, respectively, without compromising the expected merit of the future progeny (OF4) or, alternatively, it would be possible to increase the expected merit of the future progeny and, concomitantly, reduce coancestry and inbreeding (OF5 and OF6).

In scenario 3 (Table 4), the dams were kept the same as in the real scenario and 330 candidate sires were considered. As for OF3, the genetic merit was maximized when the top 28 sires were mated with four dams each, and the remaining (302) sires were not used (OF7). The expected merit of the future progeny was higher for OF7 than for OF3, because more candidate sires were available, providing more opportunity for the algorithm to find alternative mates to optimize the objective function. As for OF5 and OF6, results from OF10 showed that, compared to the real scenario, the algorithm for MS allowed to

reduce coancestry and inbreeding with a concomitant increase in the expected merit of the future progeny.

Table 4. Genetic merit, coancestry and inbreeding results from the optimization of different objective functions in coho salmon.

OF	w_1	w_2	w_3	nSire	x'EBV	x'Ax	$\overline{F}$	dif_Index	dif_x'Ax	dif_$\overline{F}$
Real	-	-	-	61	2.74025	0.17639	0.08130	0.0	0.0	0.0
Scenario 1: Maximize and minimize inbreeding*										
1	0	0	-1	61	2.74025	0.17639	0.06894	0.0	0.0	-15.25
2	0	0	1	61	2.74025	0.17638	0.12667	0.0	0.0	55.84
Scenario 2: Sire use optimization**										
3	1	0	0	28	2.89665	0.17798	0.08378	5.71	0.91	3.08
4	0	-100	-10	47	2.73764	0.17078	0.06811	-0.10	-3.17	-16.24
5	1	-50	-1	42	2.80045	0.17146	0.06674	2.19	-2.78	-17.96
6	1	-20	-1	37	2.85372	0.17335	0.06711	4.14	-1.70	-17.47
Scenario 3: Alternative mates***										
7	1	0	0	28	2.94849	0.18981	0.08737	7.60	7.60	7.50
8	0	-100	-10	89	2.62786	0.16045	0.06523	-4.10	-9.07	-19.80
9	1	-50	-1	84	2.70951	0.16098	0.06500	-1.12	-8.73	-20.05
10	1	-20	-1	80	2.78876	0.16360	0.06636	1.77	-7.26	-18.33

OF, objective function; w_1, w_2 and w_3, weights for genetic merit, coancestry and inbreeding, respectively; nSire, number of selected sires; x'EBV, genetic merit; x'Ax, coancestry; $\overline{F}$, inbreeding; dif_Index, difference of expected genetic merit (index) in percentage; dif_x'Ax, difference of coancestry in percentage; dif_$\overline{F}$, difference of inbreeding in percentage.

dif_Index, dif_x'Ax and dif_$\overline{F}$: are compared to the respective results from the Real scenario.

*The sires, dams and their intensity of use, were kept equal to the real scenario

**Sires and dams were kept the same as in the real scenario, but the sires were allowed to be mated with zero to four dams.

*** The dams were the same as in the real scenario, but candidate sires were the three best males per family from the year 2010 (total of 330 candidate sires).

2.4 Discussion

To perform MS in aquaculture breeding, a DE algorithm (Storn & Price, 1995), was applied under different scenarios, in two real datasets from Nile tilapia and coho salmon breeding populations. The algorithm showed to be computationally efficient in terms of processing speed and memory requirement (data not shown), making it suitable for practical applications. The computational efficiency came mainly from the use of Colleau (2002) indirect approach to compute coancestry and linked lists (Knuth, 1975) to store and operate the sparse matrices. For instance, the analyses OF4 to OF6 of the coho salmon dataset, which had 573 animals (candidates and their ancestors) to compute coancestry, run in approximately 10 minutes in a PC with an Intel® Core™ i7 2.2GHz processor and 8GB RAM. Simpler OF resulted in faster analyses, especially if inbreeding of the future progeny was not accounted for (w_3=0). For example, OF3 of the coho salmon dataset, which accounted just for the genetic merit, was optimized in less than 2 seconds.

Besides being computationally efficient, the MS algorithm showed to be flexible regarding the components to be considered in the OF to be optimized. The definition of the proper weight for each component depends on several factors, including: number of families (effective population size); current level of inbreeding and, more importantly, current level of coancestry among candidates; the allowed reduction of the genetic progress in the short term; the maximum desired rate of inbreeding; and the time horizon being considered. In the applied MS algorithm the weights for the different components of the OF need to be determined empirically. In contrast, the analytical derivation of OC selection using LaGrangian multipliers (Meuwissen, 1997) automatically provides the optimum genetic contribution, under constrained rate of inbreeding, without the necessity to define the weights for genetic merit and coancestry *a priori*. This disadvantage of the applied MS algorithm can be compensated by running several analyses varying the weights for the different components of the OF what, in turn, allows to explore the potential outcomes, enabling to better balance the different components and to make the selection

and mating decisions in a more dynamic and tactical way (Kinghorn & Shepherd, 1999). In scenario 2 of Nile tilapia, for example, different weights for coancestry were tested allowing assessing which set of weights resulted in a significant reduction of coancestry without expressively reducing the genetic merit.

Another aspect of the MS algorithm is that, for being based on an evolutionary algorithm, it is not guaranteed to provide the optimum solution. Because of the stochastic nature of evolutionary algorithms and depending on the complexity of the function to be optimized, a local optimum can be provided as the solution of the optimization process instead of the optimum solution. However, the DE algorithm (Storn & Price, 1995) used in the present study is advocated to be very powerful to optimize diverse objective functions studied in the literature (Price et al.; 2005; Carvalheiro et al.; 2010; Kinghorn, 2011). OC selection can also be applied using semidefinite programming (Pong-Wong & Woolliams, 2007; Hely et al.; 2012) that, according to Pong-Wong & Woolliams (2007), guarantees the finding of the optimum solution. The comparison between different optimization methods was outside the scope of the present study.

Although our results focused just on the expected genetic merit and inbreeding of the next generation, they are in accordance with the results from the literature showing the superiority of OC selection over selection based exclusively on genetic merit, in terms of maximizing the genetic gain under controlled rate of inbreeding (Meuwissen, 1997; Meuwissen & Sonesson, 1998). Also, compared to the selection based exclusively on genetic merit, MS results showed the possibility to reduce coancestry and inbreeding without compromising the expected merit of the future progeny or, alternatively, to increase the expected merit of the future progeny and, concomitantly, reduce coancestry and inbreeding. This result highlights the great flexibility of the MS algorithm. Evidence was found that MS outperformed OC selection followed by minimum inbreeding mating in controlling inbreeding, under similar levels of genetic merit and coancestry. A simulation study applying both strategies over subsequent generations is recommended for a better comparison.

Compared to truncation selection or to the real mates, MS allowed a greater reduction of coancestry and inbreeding for the Nile tilapia (Table 3: OF12 and OF13) than

for the coho salmon population (Table 4: OF9 and OF10). This result can be associated to the smaller number of controlled generations and lower level of coancestry and inbreeding of the Nile tilapia population, providing more opportunity for the algorithm to find alternative candidates and mates to optimize the OF and to attain better outcomes for the components of the OF. This highlights the importance of adopting strategies to control inbreeding since the establishment of the breeding programs. It is important to emphasize that the empirical commonly used strategies for controlling inbreeding in aquaculture, as restricting the number of selected animals per family and not allowing full and half-sib mates, can be useful in the beginning of the breeding program but are not effective in the long term (Skaarud et al.; 2011; Yáñez et al.; 2014a). In the case where some of the broodstock are used for production or multiplication coancestry and inbreeding could be just ignored, e.g. OF1 (Table 3), thus maximizing the genetic gain. The algorithm also allow to set specific values for coancestry (w2) and inbreeding (w3), in the case the broodstock manager needs to account for these two parameters to generate fish for production. Besides advocating the use of OC selection and planned mates to better control the rate of inbreeding and the effective population size, Yáñez et al. (2014a) also recommended the use of genetic material to connect different genetically improved populations by using, for example, cryopreserved sperm from selected males. Unfortunately, the use of external genetic material is not always possible in aquaculture breeding programs due to commercial and sanitary barriers.

2.5 Conclusions

The mate selection algorithm was computationally efficient and flexible for practical applications in aquaculture breeding. The expected consequence of using the algorithm, in contrast with empirical procedures for controlling inbreeding, is to control inbreeding more effectively and promote higher genetic progress in the long term. Evidence was found that inbreeding can be better controlled by mate selection than by optimum contribution selection followed by minimum inbreeding mating.

Acknowledgments

The authors are grateful to Fundação do Amparo à Pesquisa do Estado de São Paulo (FAPESP, process number 2014/20626-4 and 2015/25232-7) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the financial support, and PeixeGen research group in Brazil and Aquainnovo in Chile for providing the datasets.

Conflicts of interest

The authors declare that they have no conflict of interest.

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CHAPTER 3 - Mate selection allows changing the genetic variability of the future progeny while controlling inbreeding

Abstract – this study aims to compare results obtained by mate selection accounting for different components in the objective function (OF), including the genetic variability of the future progeny, using Nile tilapia and coho salmon real datasets. A total of 8,782 Nile tilapias (NP) from five generations and 79,144 coho salmon (CS) from eight generations were used to optimize OF accounting for coancestry of parents, expected genetic merit, inbreeding and components associated to genetic variability of the future progeny. The candidates for selection were the superior animals of the last generation, corresponding to 281 males for NP population and 328 males for CS population, to be mated with 179 and 440 superior females, respectively. Candidate males were allowed to be mated with a maximum of four females. Different components related to genetic variability of the progeny were tested and we suggested the use of OF5 and OF6 when the objective is maintain the genetic variability or to produce more uniform animals, respectively, for both species. In addition, the OFs also increased number of outstanding superior progeny. The tested OF were effective in optimizing the genetic gain and keeping the coancestry and inbreeding at controlled rates, while reducing or increasing the genetic variability of progeny, depending on the purpose of production.

Keywords: breeding program, coancestry, inbreeding, genetic gain, *Oncorhynchus kisutch, Oreochromis niloticus*

3.1 Introduction

Maintenance of genetic variation within a breeding program is essential for long-term, sustainable genetic improvement of fish (Kause et al., 2014). However, selection of breeders from a small number of families and high selection intensity could reduce the genetic variability of the population, increase rates of inbreeding and reduce the genetic progress (Gjedrem, 2005). In contrast, the maintenance of genetic variability in breeding programs contradicts the practical aims of commercial producers. In tilapia production, for instance, commercial farmers are usually awarded for selling more fish within the preferred weight range (Khaw et al.; 2016). Growth uniformity is preferable at commercial level since it allows to deliver more uniform product, harvest a larger proportion of the population at market size, and reduce the need of size grading and multiple harvests (Gilmour et al., 2005; Janhunen et al., 2012a, 2012b). Furthermore, more uniform growth may also reduce competitive interactions between animals, which contributes to reduce feed monopolization and dominant behavior, and thus improve well-being of fish (Baras and Jobling, 2002).

The increasing demand from consumers and commercial farmers for uniformity of production is one of the driving forces for animal breeders to emphasize more this criterion in the selection process (Sae-Lim et al.; 2012). Some studies quantified the genetic variation for uniformity and they concluded that there is a potential to increase uniformity of production by selective breeding in Nile tilapia (Khaw et al., 2016; Marjanovic et al., 2016; Moreno et al., 2012; Omasaki et al., 2017) and in salmonids (Jakobsen et al., 1987; Sae-Lim et al., 2017, 2015, 2012). In addition, different strategies can be used to reduce variability in aquaculture species, such as the use of monosex fish (Beardmore et al., 2001), grading the fishes at several stages during the grow-out phase (King et al., 2006) and performing planned mating (Hohenboken, 1985).

Genetic variability of progeny could also be accounted for by mate selection (Piyasatian and Kinghorn, 2003). In mate selection, the selection and mate allocation decisions are performed simultaneously and components such as genetic merit, inbreeding and co-ancestry are usually considered in the objective function to be optimized (Shepherd and Kinghorn, 1999). Components related to genetic variability could

also be accommodated (Piyasatian and Kinghorn, 2003), to increase or reduce the genetic variability of the future progeny according to the interest, being of great importance to both selection nuclei and multipliers due to the arguments described previously. The benefit of using this strategy is that relevant components to be considered in a breeding program could be optimized simultaneously, decreasing the chance of finding a suboptimal solution for selection and mating decisions. It is unclear, however, in which extend accounting for genetic variability of the progeny would affect the other components to be optimized.

The present study aims to compare the results obtained for mate selection accounting to different components in the objective function, including the genetic variability of the future progeny, in real Nile tilapia and coho salmon datasets.

3.2 Material and Methods

3.2.1 Nile tilapia dataset

The dataset used in this study contained pedigree information and standardized estimated breeding values (sEBV) for harvest weight of 8,782 Nile tilapias from five generations (Table 1), provided by PeixeGen Research Group (Universidade Estadual de Maringá, Maringá, PR, Brazil).

The animals evaluated in each generation were produced using natural mating and were obtained from a mate design using two females per male. Inspection of the presence of spawning was done two times per week in the breeding season (from November to February). When the spawning was identified, the sire was removed from the hapa and the dam and the larvae were kept together until the end of breeding season. After that, 100 fingerlings from each family were divided into two equal groups and transferred for nursery structure until the average weight of about 10 grams, when 50 animals per family were individually identified. After the identification, the animals were transferred to the grow-out system in cages where they were weighted with approximately 7 months of age.

Table 1. General information, inbreeding coefficient and standardized estimated breeding value for harvest weight of Nile tilapia, per generation.

Gen	Number				Inbreeding			sEBV±SD
	Sires	Dams	Families	Progeny	Mean	Min.	Max.	
1	24	33	33	1,731	0	0	0	-0.01±1.11
2	40	57	58	1,717	0	0	0	0.07±0.55
3	52	79	79	2,695	0	0	0	0.39±0.71
4	39	44	50	1,127	0.00319	0	0.06300	0.83±1.01
5	29	42	51	1,455	0.00016	0	0.00800	0.97±1.28

sEBV, standardized estimated breeding value; SD, standard deviation; Gen, generation; Min, minimum; Max, Maximum; sEBV = EBV/83.036.

More details about the origin, family and reproduction structure of the Nile tilapia population were described by Oliveira et al. (2016) and Yoshida et al. (2017).

3.2.2 Coho salmon dataset

The coho salmon dataset used in this study contained pedigree information and standardized economic index (sIndex) of 79,144 coho salmon from the even population of AquaChile Breeding Program in Chile, comprising eight generations (Table 2).

The spawning was induced using hormone and all families were generated within one or two weeks using three to five females per male as mate design. The eggs of each full-sib family were incubated separately, and at eyed stage 2,000 eggs of each selected family were moved to individual tanks (400 l each) until they weighted about 5 to 7 g when the animals were identified individually using PIT (Passive Integrated Transponder) tags. Then, 60 to 80 animals per family were transferred into two to three smoltification cages in fresh water conditions. Smoltification occurred naturally at eight months post-spawning and the weight at harvest time (~3 kg) was recorded at 20–21 months of age. More details about this population can be seen at Dufflocq et al. (2016) and Yañez et al. (2014, 2016).

Table 2. General information, inbreeding coefficient and standardized economic index for coho salmon, per generation.

Gen	Number				Inbreeding			sIndex±SD
	Sires	Dams	Families	Progeny	Mean	Min	Max	
1998	42	81	81	8,619	0.000	0.000	0.000	-0.05±0.23
2000	36	73	73	6,557	0.002	0.000	0.125	0.37±0.30
2002	59	114	114	9,120	0.025	0.000	0.125	0.63±0.38
2004	49	137	137	10,761	0.047	0.000	0.172	1.32±0.31
2006	37	102	102	10,523	0.062	0.016	0.203	1.65±0.37
2008	34	98	98	8,821	0.063	0.027	0.191	1.97±0.33
2010	45	110	110	8,798	0.070	0.035	0.126	2.37±0.28
2012	61	112	112	15,945	0.081	0.056	0.162	2.74±0.36

sIndex, standardized economic index; SD, standard deviation; Gen, generation; Min, minimum; Max, Maximum; sIndex = Index/6.79329.

3.2.3 Objective function

The mate selection (MS) was defined with the optimization of the following objective function (OF):

$$OF = w_1 x'EBV + w_2 x'Ax + w_3 \bar{F} + w_4 Ntop + w_5 vEBVt + w_6 vEBVb$$

where, x'EBV is the expected merit of the future progeny; x'Ax is the weighted mean coancestry of selected parents; $\bar{F}$ is the expected average inbreeding coefficient of the future progeny; Ntop is the number of animals in the future progeny with expected genetic merit (mean of parents' EBVs) greater than 3 genetic standard deviations for Nile tilapia and greater than 3.5 for coho salmon, aiming at producing a greater proportion of outstanding (superior) animals; vEBVt and vEBVb are, respectively, mean deviation of sEBV (sIndex) to the cube of future progeny of females classified as 50% higher (vEBVt) and 50% lower (vEBVb), favoring the occurrence of positive associative (vEBVt) and corrective (vEBVb) matings; w_1 to w_6 are the corresponding weighting factors and x is the vector to be optimized of genetic contributions for each candidate (the symbol ' denotes a transposed vector).

The weights w_1 to w_3 were defined in a previous study, with values that presented the best results in terms of genetic merit maximization and inbreeding control for Nile tilapia (OF1: $w_1 = 1$, $w_2 = -20$, and $w_3 = -1$, Yoshida et al., 2017) and for coho salmon (OF1: $w_1 = 1$, $w_2 = -100$ and $w_3 = -1$, Yoshida et al., 2016). Different values for the other three weights (w_4 to w_6) that considered the genetic variability of the progeny were tested (Tables 2 and 3) and compared to the OF that assumed null values for w_4 to w_6 (OF1).

The components $\overline{F}$, Ntop, vEBVt and vEBVb, when included in the OF, determined the mate allocations indirectly following the problem representation proposed by (Gondro and Kinghorn, 2008), which uses an auxiliary vector of real numbers representing the "rankings" (order) of mates to be performed (Gondro and Kinghorn, 2008; Shepherd and Kinghorn, 1998). This auxiliary vector of real numbers was optimized together with x vector. The objective functions were optimized using a differential evolution algorithm developed in FORTRAN language (Carvalheiro et al., 2010a, 2010b).

For Nile tilapia, the best four females (179 animals) and six males (281 animals) per family of the fifth generation were considered as selection and mate candidates, excluding the animals with negative EBV. For coho salmon, the top three males (328) and four females (440) with positive economic index from 112 families of the class-year 2012 were considered as selection and mate candidates. For both species, each candidate female was mated once (i.e. female contribution was not optimized) and the males were allowed to be mated with a maximum of four females.

3.3 Results

3.3.1 Nile tilapia

The optimization of the objective functions for mate selection, considering components related to genetic variability of the future progeny (OF2 to OF7), indicated that the applied algorithm allowed to change the standard deviation (SD) of expected sEBVs of the future progeny, while keeping genetic merit, coancestry and inbreeding at similar levels to those of OF1 (Table 3).

The lowest and highest SD were observed, respectively, by the optimization of the objective function that favored the occurrence of corrective (OF5, SD = 0.246) and positive

associative (OF4, SD = 0.771) mating. These mates (OF5 and OF4) presented the lowest (0.3%) and highest (2.4%) average inbreeding value of the future progeny, respectively (Table 3).

The optimization of OFs considering Ntop were effective in increasing the expected number of outstanding (superior) progeny in comparison with OFs not using Ntop. The greatest Ntop value was observed by OF2 and OF3 (Ntop = 64) and the lowest by OF5 (Ntop = 7) that, as described previously, favored the occurrence of corrective mating. Except for OF4, the number of sires selected was similar among OF (Table 3).

Table 3. Weights (w_1-w_6) applied to the different objective functions (OF1-7), respective optimized results for the expected genetic merit of the future progeny (x'EBV) and its standard deviation (SD), coancestry (x'Ax), inbreeding of the future progeny ($\bar{F}$), expected number of outstanding progeny (Ntop) and number of sires selected (nSire), for mate selection in Nile tilapia.

OF	w_1	w_2	w_3	w_4	w_5	w_6	x'EBV	SD	x'Ax	$\bar{F}$	Ntop	nSire
1	1	-20	-1	0	0	0	2.434	0.477	0.025	0.005	23	72
2	1	-20	-1	1	0	0	2.432	0.601	0.026	0.012	64	74
3	1	-20	-1	1	0	1	2.473	0.497	0.028	0.009	64	68
4	1	-20	-1	0	1	0	2.357	0.771	0.029	0.024	34	94
5	1	-20	-1	0	0	1	2.455	0.246	0.027	0.003	7	70
6	1	-20	-1	0.01	0.01	0.01	2.446	0.653	0.026	0.007	35	70
7	1	-20	-1	1	1	1	2.458	0.642	0.030	0.011	36	70

The distributions of the expected genetic values of the future progeny (Figure 1) reinforce the results presented in Table 3. In comparison with OF1, a greater dispersion of sEBVs was observed for OF4, where there is a higher proportion of animals with upper and lower extreme sEBVs, resultant from the associative positive mating favored by considering vEBVt in the OF to be optimized. OF5 presented a higher proportion of progeny with expected genetic merit around the mean, as the component vEBVb favored the occurrence of corrective mating. In addition, it is possible to observe that OF2 and

OF3 were effective in increasing the expected proportion of progeny with sEBV above three genetic standard deviations (Figure 1A). When considering simultaneously the three components related to progeny variability (OF6 and OF7), there was an increase in the frequency of animals with extreme upper and also lower sEBVs compared to OF1 (Figure 1B). However, the increase in extreme lower sEBVs of OF6 and OF7 was not as pronounced as that presented by OF4, which did not consider vEBVb.

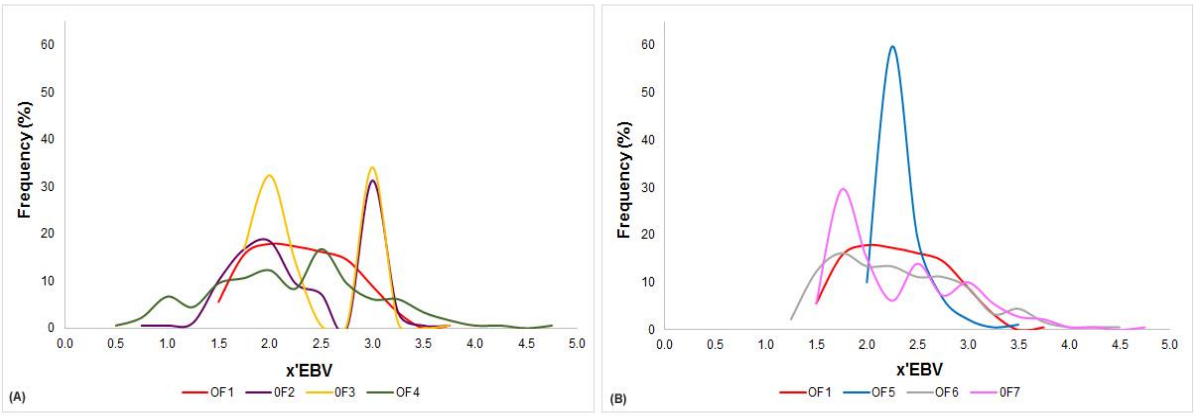

Figure 1. Distribution of expected genetic merit of the future progeny according to different objective functions (OF) for mate selection accounting (OF2 to OF7) or not (OF1) for the genetic variability of the future progeny, in Nile tilapia.

3.3.2 Coho salmon

The coho salmon population also confirmed the result that considering the genetic variability of the future progeny on mate selection (OF2 to OF7) allows changing the dispersion of the expected genetic merit of the future progeny without compromising genetic gain, coancestry and inbreeding, in comparison to OF1 (Table 4).

OF2 and OF3 were very effective in increasing the expected number of outstanding animals, providing a 5 fold increase on Ntop compared to OF1 (Table 4). OF4, which favored positive assortative mating, also allowed increasing the expected proportion of outstanding progeny but, differently from Nile tilapia, presented similar distribution for lower sEBVs than OF1 (Figure 2). It is important to note that the expected genetic merit

of the future progeny for OF4 was slightly lower than OF1 for Nile tilapia (Table 3), the opposite occurring for coho salmon (Table 4).

Similarly as in Nile tilapia, OF5 presented a lower dispersion of the expected genetic merit of the future progeny compared to the other OFs in the coho salmon population. The OFs which considered simultaneously all the components related to progeny variability (OF6 and OF7) also presented in coho salmon a good compromise in increasing the expected proportion of outstanding progeny while keeping the other components similar to those of OF1 (Table 4 and Figure 2).

Table 4. Weights (w_1-w_6) applied to the different objective functions (OF1-8), respective optimized results for the expected genetic merit of the future progeny (x'EBV) and its standard deviation (SD), coancestry (x'Ax), inbreeding of the future progeny ($\bar{F}$), expected number of outstanding progeny (Ntop) and number of sires selected (nSire), for mate selection in coho salmon.

OF	w_1	w_2	w_3	w_4	w_5	w_6	x'EBV	SD	x'Ax	$\bar{F}$	Ntop	nSire
1	1	-100	-1	0	0	0	3.163	0.232	0.151	0.079	22	145
2	1	-100	-1	1	0	0	3.174	0.293	0.151	0.091	118	142
3	1	-100	-1	1	0	1	3.183	0.265	0.151	0.085	117	139
4	1	-100	-1	0	1	0	3.233	0.279	0.155	0.087	75	184
5	1	-100	-1	0	0	1	3.167	0.145	0.151	0.079	10	145
6	1	-100	-1	0.01	0.01	0.01	3.169	0.299	0.151	0.081	64	143
7	1	-100	-1	1	1	1	3.235	0.275	0.155	0.089	82	174

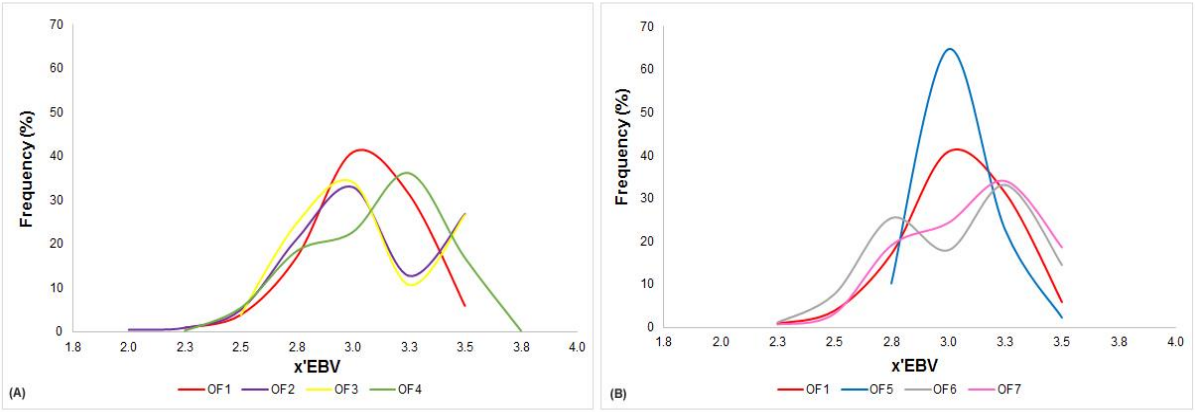

Figure 2. Distribution of expected genetic merit of the future progeny according to different objective functions (OF) for mate selection accounting (OF2 to OF7) or not (OF1) for the genetic variability of the future progeny, in coho salmon.

3.4 Discussion

It is notable that the use of the components of genetic variability in the objective function allowed changing the variability of the progeny by directing the mating according to the proposed objective. In Nile tilapia, the use of mate selection was more effective in promoting the change on genetic variability of the future progeny compared to coho salmon (Table 3: OF4 and OF5 vs Table 4: OF6 and OF5). This occurred probably because the coho salmon population is more inbred than the Nile tilapia population. Thus, the algorithm has a smaller parametric space to explore the genetic variability of the progeny while keeping inbreeding controlled.

It should be noted that there is no general rule for choosing the weights and the definition of the best values for the weights related to progeny variability will depend on the purpose of the use of the animals. In this way, the animals could be intended for use in breeding programs or as multipliers. An alternative to be further investigated would be to modify the algorithm to also optimize the weights. This, however, would probably characterize a multi-objective optimization problem with conflicting objectives, without a global optimum solution (Abbass, 2000).

In breeding programs, the genetic gain achieved by selective breeding depends on the presence of additive genetic variation in the population. In this way, the success of a

selective breeding program will depend on the genetic variation in the base population, as well as how the population is maintained from one generation to the next (Puttaraksar, 2004). Some authors (Bijma, 2000; Hill, 1979; Smitherman, 1987) suggested that an effective population size equal to at least 50 to 150 would allow controlling inbreeding and maintaining the genetic variability of breeding programs.

The problem of inbreeding accumulation over the generation is the reduction on performance of traits directly and indirectly (Gjedrem, 2005). In this way, for nuclei of breeding programs is desired the optimization of the genetic progress, controlling the coancestry, inbreeding and maintaining genetic variability. In this case, the optimization of functions like OF6 ($w_4=w_5=w_6=0.01$) seems to be the most indicated for Nile tilapia and coho salmon.

On the other hand, practical alternatives are commonly used by fish farmers to reduce the variability as grading the animals several times during the grow-out phase, but this is harmful to fish welfare and increase the mortality rate due of the stress after the this manipulation, besides increasing the labor costs (Garcia et al., 2013; King et al., 2006). In this way, when the purpose for the use of the animals is the dissemination of improved breeders, in order to use them as multipliers, we want to reduce the variability to increase the uniformity of growth and increase the productive efficiency. In this case, a function like OF5 would be better for both species. It should be noted that, for all mating strategies, the phenotypic variability of the future progeny would also depend on the variance of non-additive effects, environmental effects and the variance related to Mendelian segregation, responsible for half of the additive genetic variance (Neves et al., 2009).

In a previous study, we showed that the mate selection algorithm was computationally efficient and flexible for practical applications in aquaculture breeding when the expected merit of the future progeny, the coancestry and the inbreeding were used as components to be considered in the optimization of the objective function. Mate selection showed to be efficient in maximizing genetic progress while controlling coancestry and inbreeding for both Nile tilapia and coho salmon populations (Yoshida et al.; 2017). In the current study, we accounted for components related to genetic variability in the optimization of the OF and the results showed that the genetic variability of the

progeny can be shaped, depending on the objective to use the animals, without compromising the other components of the OF. It would be interesting to perform a simulation study to investigate the consequences on long-term inbreeding and genetic progress of applying mate selection accounting for genetic variability.

3.5 Conclusions

The mate selection algorithm accounting for genetic variability was effective in directing the mattings to produce animals with higher or lower expected genetic variability, depending on the purpose of the use of the animals and, at the same time, in maximizing genetic progress under controlled inbreeding.

Acknowledgments

The authors are grateful to PeixeGen research group in Brazil and Aquainnovo in Chile for providing the datasets. GMY acknowledge Fundação do Amparo à Pesquisa do Estado de São Paulo (FAPESP, process number 2014/20626-4 and 2015/25232-7) for doctoral fellowship and RC acknowledge Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, process number 308636/2014-7) for fellowship.

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CHAPTER 4 - Mate selection in aquaculture breeding using simulated data

Abstract - The objective of this study was to compare mate selection (MS) among truncation selection (TS) and optimum contribution selection (OCS) scenarios combined to different mating strategies (random mating and minimizing inbreeding level) to assess the best method in controlling inbreeding and maintain the genetic gain, for aquaculture breeding using simulated dataset. Twenty discrete generations were simulated, considering 50 families and 2,000 offspring per generation, and a trait with heritability of 0.3. The TS, OCS and MS were applied using a Differential Evolution algorithm, under an objective function that accounted for genetic merit, inbreeding of the future progeny and co-ancestry among selection candidates. For TS and OCS, the selection was based in the optimization of the respectively objective function and the mates were considered as random mating or minimized the inbreeding level. For MS, the objective functions using different weights for coancestry were tested. For each application, 20 replicates were simulated and the results were compared based on their average. Our results showed that, inbreeding level can be better controlled by MS than by truncation selection and OCS followed by random mating. In the short-term, MS was more efficient than OCS + inbreeding minimizing in controlling inbreeding under the same genetic gain. However, in the long-term, OCS and MS resulted in similar genetic progress and average inbreeding, under the same weight on coancestry.

Keywords: Differential Evolution, coancestry, inbreeding, genetic gain, optimum contribution selection, truncation selection

4.1 Introduction

Selective breeding schemes for animals involve two steps: selection and mating. Selection is choose the animals to be used as parents for the next generation and mating is pair the selected parents to produce the offspring of the next generation (Henryon et al., 2009). The mate step have the largest impact on the most breeding programs, because will determine the genetic contribution of each parent and the inbreeding level in long term (Henryon et al., 2009; Sonesson and Meuwissen, 2000). In most fish species, this step is a problem due the high fecundity facilitates, that will result in high selection intensity, which enables relatively high annual genetic gain. Furthermore, this can also potentially lead to very few families dominating the genetic contributions to the next generation and, consequently, the rate of inbreeding can easily become increased to undesirable levels (Caballero et al., 1996). In contrast, implementing mating criteria that pair the selected parents appropriately can further improve genetic gain and/or reduce inbreeding (Henryon et al., 2009). High rates of inbreeding in selection programs may have an important effect on medium- and long-term response to selection, as may increase the manifestation of deleterious alleles, cause inbreeding depression reducing the probability of fixing favorable genes, reduce genetic variation and, consequently, the genetic progress of subsequent generations (Falconer and Mackay, 1996).

Different selection methods for breeding programs have been recent proposed as optimum contribution selection (OCS) (Meuwissen, 1997; Woolliams and Thompson, 1994) that maximize genetic response while constraining inbreeding by restricting the coancestry among the parents. The OCS is usually applied with the combination of mating strategies as random mating, minimum coancestry and compensatory mating strategies (Caballero et al., 1996; Carvalheiro et al., 2010a; Grundy et al., 1998; Sonesson and Meuwissen, 2000). In contrast, simultaneous selection and mate allocation strategy of animals entering in a breeding program have been proposed by Kinghorn and Shepherd (1999) and Shepherd and Kinghorn (1999) by use of mate selection strategies (MS).

The mate selection analysis, results in a mating list with incorporated decisions on breeding objectives, e.g. selection pressure, genetic gain, genetic diversity, progeny inbreeding, crossbreeding, use of reproductive technologies, which animals to take

cryopreserved semen, etc. (Kinghorn, 2011). This list of components evaluated constitute the overall mate selection objective function and the challenge is to find the mating set that gives the best solution for the objective function (Kinghorn and Shepherd, 1999). For this purpose, some algorithms have been advocated for finding the optimum solution, as semidefinite programming (Pong-Wong & Woolliams, 2007; Hely et al.; 2012), linear programming (Jansen and Wilton, 1985; Toro et al., 1988; Toro and Pérez-Enciso, 1990; Weigel and Lin, 2000), and simulated annealing (Fernández et al., 2001; Toro and Varona, 2010). However, Storn and Price (1997) suggested the use of Evolutionary algorithm based on Differential Evolution (DE) that mimic biological evolution in their quest to find the best solution for a complex optimization problem.

In a mate selection study, Carvalheiro et al. (2010b) implemented the DE for the optimization of the objective function using different components, as genetic merit, inbreeding and coancestry of the future progeny. In order to increase the speed and feasibility of the program, was adopted an indirect approach to calculate the coancestry (Colleau, 2002). This algorithm present some advantages as simple structure, computationally efficient, has good properties of convergence, easy to implement and robust (Carvalheiro et al., 2010a;b; Gondro and Kinghorn, 2008). Some studies were conducted using DE for mate selection (Carvalheiro et al., 2004; Carvalheiro, 2010b; Hayes et al., 2002; Kinghorn and Shepherd, 1999; Kinghorn, 2011, 1998; Li et al., 2006; Shepherd and Kinghorn, 1998) and showed to be efficient in optimized the components considered in the objective function. Using real Nile tilapia and coho salmon datasets, Yoshida *et al.* (2017) observed evidence that MS outperformed OCS in controlling inbreeding under the same expected genetic gain in the short-term.

The objective of this study was to compare the mate selection (MS) algorithm among truncation selection (TS) and optimum contribution selection (OCS) scenarios under different mating strategies (random mating and minimizing inbreeding level), to assess the best method in controlling inbreeding and maintain the genetic gain in long-term, for aquaculture breeding using simulated dataset.

4.2 Material and Methods

4.2.1 Simulated data

The animals from base population (G0) was formed with 25 males and 50 females. Genetics values were simulated according to Bulmer (1985). Genotypes, g_i, were sampled from the distribution N(0, σ_a^2), where σ_a^2 is the genetic variance in G0. Phenotypes in the base population were then calculated from:

$$y_i = g_i + e_i$$

where, e_i is the environmental effect sampled from N(0, σ_e^2), with σ_e^2=1−σ_a^2. This in the base generation the phenotypic variance was equal to 1 and the heritability (σ_a^2=h^2=0.30). Phenotypic values of the offspring in later generations were generated as:

$$y_i = 0.5g_s + 0.5g_d + m_i + e_i$$

where g_s and g_d are the additive genetic values of the sire and dam, respectively; m_i is the Mendelian sampling effect with the distribution N(0, 0.5(1−(F_s+F_d)/2)σ_a^2), with F_s and F_d being the inbreeding coefficients of the sire and dam, respectively; and e_i is the environmental effect sampled from N(0, 1−σ_a^2). We simulated 20 discrete generations (19 generations of selection) with 20 repetitions/generation, the same number of individuals for each generation (n = 2,000) and equal number of males and females.

4.2.2 Objective function

A mate selection algorithm based on Differential Evolution (DE – Storn & Price, 1995) was developed in FORTRAN language by Carvalheiro et al.; (2010b).The selection and mates were defined using the following mate selection objective function (OF):

$$OF = w_1 x' EBV + w_2 x' Ax + w_3 \bar{F}$$

where, x'EBV is the expected merit of the future progeny; x'Ax is the weighted mean coancestry of selected parents; $\bar{F}$ is the expected average inbreeding coefficient of the future progeny; w_1 to w_3 are the corresponding weighting factors and x is the vector to be optimized of genetic contributions for each candidate (the symbol ' denotes a transposed vector).

For each discrete generation, it was considered as selection and mate candidates the best female (50 animals) and the best five males (250 animals) per family. The males were allowed to be mated with a maximum of four females and each female was mated once, i.e. the contribution of each female was not optimized.

The operational parameters of the DE algorithm to optimize the OF where: population size = 2 times the number of candidates; crossover rate = 0.5; mutation factor = 0.2 (or 0.9 every 4 generations); and maximum number of generations of the evolutionary process (maxgen) = 100,000. Convergence was assumed when the range and the mean absolute deviation of the OF, considering all the possible solutions per generation, were lower than $1x10^{-6}$. The best solution from the maxgen generation was considered as the optimum solution when the convergence criterion was not attained.

The approach proposed by Lampinen and Zelinka (1999) was adopted to provide integer solutions for the number of mates per candidate. To increase computational efficiency, Colleau (2002) indirect approach was adopted to calculate coancestry, and linked lists (Knuth, 1975) were used for the storage and calculations involving sparse matrices. The mate selection algorithm is freely available for research purpose and can be obtained under request to the corresponding author.

4.2.3 Scenarios

A total of 11 OF were tested, under five different scenarios that are presented in Table 1. The scenario 1, corresponded to the truncation selection (TS), when just the x'EBV was optimized in the OF1. The scenario 2 corresponded to truncation selection followed by the inbreeding minimizing (TS + FM), the x'EBV was optimized and the $\bar{F}$ were minimized using different weights for OF2 (w_3 = -0.00001) and OF3 (w_3 = -1). The OF4 to OF6 is the scenario 3 and they are equivalent to optimum contribution selection followed by random mating (OCS + RM). In this scenario the coancestry was minimized using different weights for w_2 (w_2= -1, -10 and -20, for OF4, OF5 and OF6, respectively). In the scenario 4, two weights were tested to coancestry (w_2= -10 and -20, for OF7 and OF8, respectively) and a small weight for $\bar{F}$ were used (w_3= -0.00001) corresponded to optimum contribution selection followed by the minimum inbreeding mating scenario (OCS + F).

The OF9 to OF11 corresponded to mate selection optimization (MS) where different weights were used to x'Ax and $\bar{F}$ (w_2= -10 or -20; w_3= -1 or -10) as observed in Table 1.

Table 1. The weight definition for each objective function (OF) in different selection and mate scenarios.

OF	w_1[1]	w_2[2]	w_3[3]
Truncation selection (TS)			
1	1	0	0
Truncation selection + inbreeding minimizing (TS + FM)			
2	1	0	-0.00001
3	1	0	-1
Optimum contribution selection + random mating (OCS + RM)			
4	1	-1	0
5	1	-10	0
6	1	-20	0
Optimum contribution selection + inbreeding minimizing (OCS + FM)			
7	1	-10	-0.00001
8	1	-20	-0.00001
Mate selection (MS)			
9	1	-10	-1
10	1	-20	-1
11	1	-20	-10

[1]Weight for expected merit of the future progeny.

[2]Weight for coancestry of selected parents.

[3]Weight for expected average inbreeding coefficient of the future progeny.

The weights used, were determined empirically, based on results from previous studies (Carvalheiro et al., 2010b; Yoshida et al., 2017). For each application, 20 replicates per generation (constituted by different populations) were simulated and their

results were averaged for the comparisons. The results were compared based on genetic gain, coancestry and inbreeding provided by each scenario.

4.3 Results

The truncation selection (OF1) resulted in high increase in coancestry and inbreeding level since the initial generations and archived values up to 0.94 and 0.44 in the 20th generation, respectively (Figure 3A and 4A). Even with the reduction in the genetic variability (ranged from 0.30 to 0.14 in the 1st and 20th generation, respectively; Figure 2A) due the higher inbreeding level, it was not enough to compromise the genetic gain, which resulted on an average of 9.03 at 20th generation (Figure 1A).

The results of OF2 and OF3 showed a reduction in the coancestry (0.89 and 0.76, respectively) and in the inbreeding level (0.41 and 0.34, respectively) compared to the truncation selection (OF1) (Figure 3A and 4A). Although the coancestry and inbreeding levels were lower than the OF1, the recommendation of mate strategy that minimizing the inbreeding was not effective in controlling it, compared to OCS and MS scenarios that account to coancestry (Figure 4A and 4B). Contrasting the OF2 and OF3, it was possible to observe that the highest importance for inbreeding in the OF3 (w3 = -1) resulted in a greater reduction in inbreeding without compromising the genetic gain (8.94 *vs* 9.26 in the 20th generation, for OF2 and OF3 respectively).

Despite the slight reduction in genetic progress (<8.66 in 20th generation), the strategies of OCS followed by random mating (OF4 - OF6) were more effective in constrain the inbreeding level, compared to truncation selection scenarios (OF1 - OF3), reinforce the importance in considered the coancestry in the OF (Figure 1A). The increase in the importance for coancestry (w_2= -1 > -10 > -20) resulted in the higher reduced in coancestry, inbreeding value and genetic progress, compared to TS and TS + MF scenarios. In contrast the genetic variability remained with higher values ranged from 0.18 to 0.25 in 20th generation, for OF4 and OF6, respectively (Figure 2A).

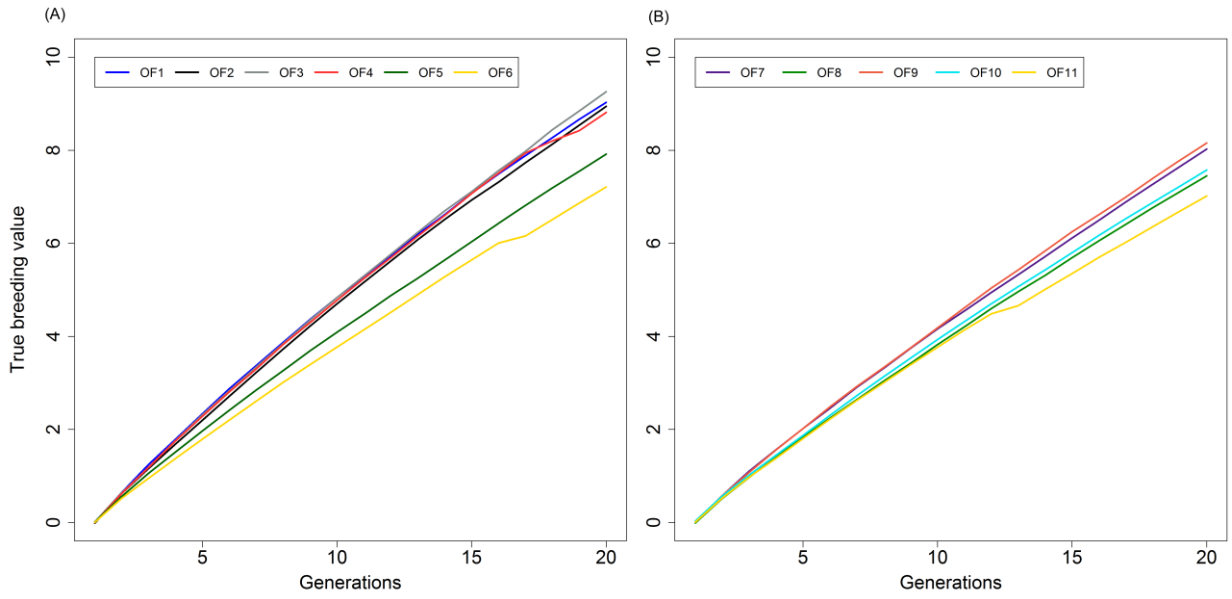

Figure 1. Average true breeding value over 20 generation when the parents are selected considered different objective function (A: OF1 to OF6; B: OF7 to OF11). The weight definition for each objective function are presented in Table 1.

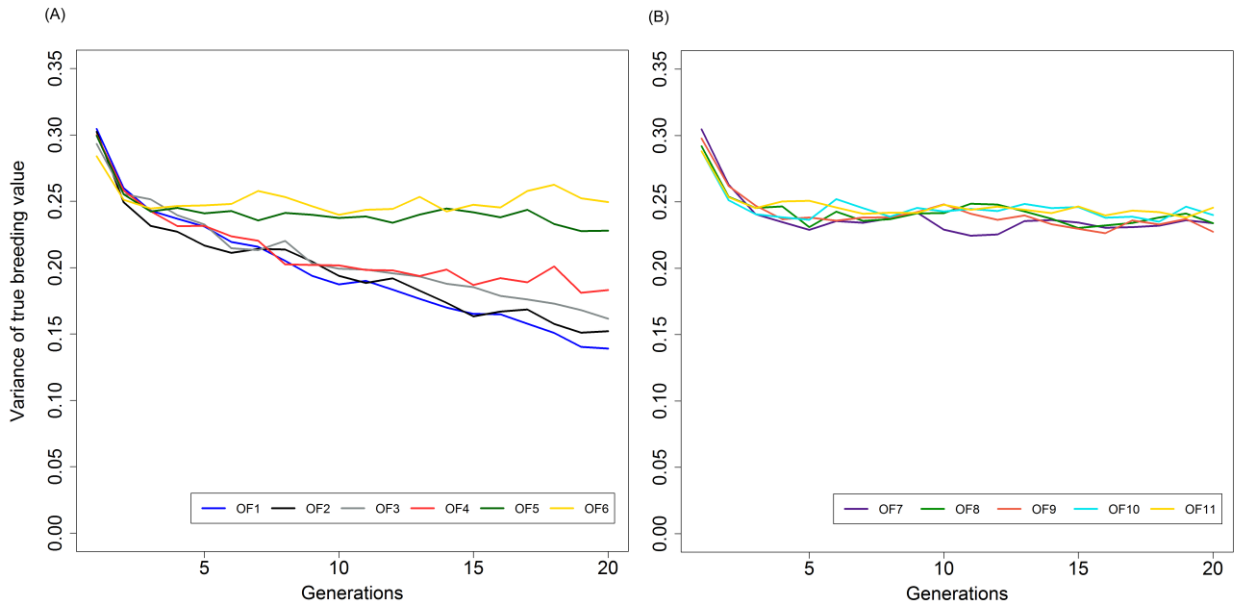

Figure 2. The variance of true breeding value over 20 generation when the parents are selected considered different objective function (A: OF1 to OF6; B: OF7 to OF11). The weight definition for each objective function are presented in Table 1.

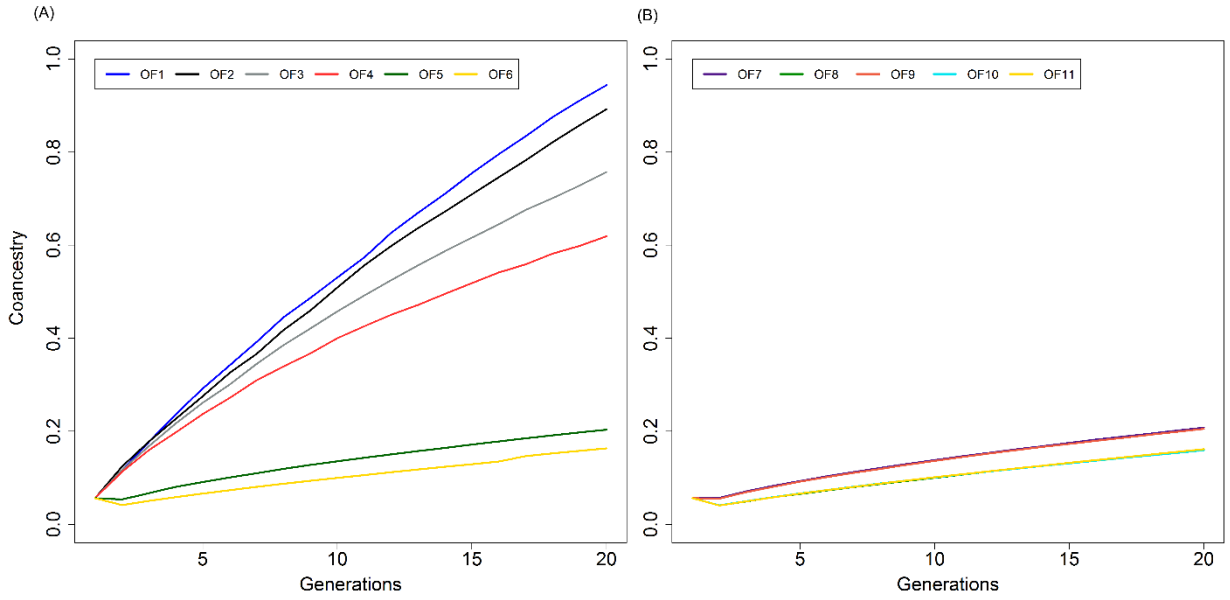

Figure 3. Average coancestry over 20 generation when the parents are selected considered different objective function (A: OF1 to OF6; B: OF7 to OF11). The weight definition for each objective function are presented in Table 1.

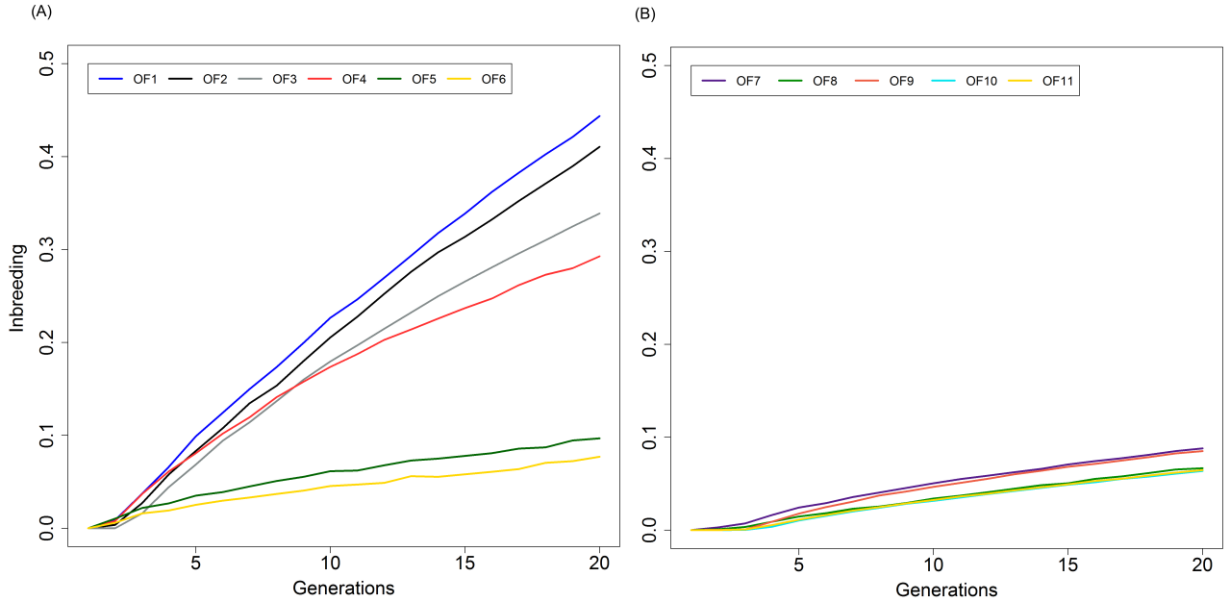

Figure 4. Average inbreeding level over 20 generation when the parents are selected considered different objective function (A: OF1 to OF6; B: OF7 to OF11). The weight definition for each objective function are presented in Table 1.

The scenario 4, corresponded to the OCS + FM (OF7 and OF8) and the results showed that this strategy was more efficient in reduction the coancestry and inbreeding (Figure 3B and 4B) with an increase in genetic progress (Figure 1B), when compared to scenario 3 (Figure 1A, 3A and 4A). In contrast, this scenario presented similar genetic gain and inbreeding level by mate selection scenario (OF9 to OF11) in long-term. The more emphasis in coancestry (OF7 and OF9 *vs* OF8 and OF10) resulted in a better control of inbreeding along the generations, with a small reduction in genetic response (Figure 1B) and in the genetic variability (Figure 2B). This result evidences that what ultimately control inbreeding in the long-term is the constraint on coancestry (Figure 4B).

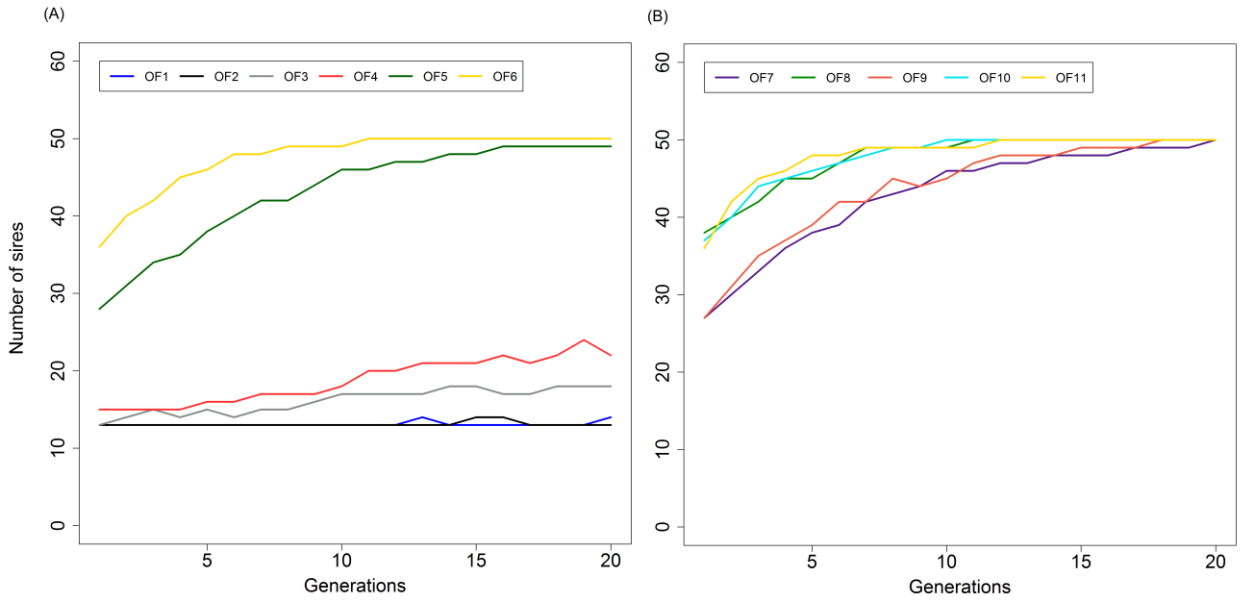

Figure 5. Average number of sires selected over 20 generation when the parents are selected considered different objective function (A: OF1 to OF6; B: OF7 to OF11). The weight definition for each objective function are presented in Table 1.

In the short-term, MS scenario was more efficient in controlling inbreeding than OCS + FM under the same genetic gain. At generation 4, for example, the average inbreeding of the different strategies was equal to 1.61% and 0.89% for OF7 and OF9, and equal to 0.88% and 0.36% for OF8 and OF10, respectively (Figure 4B).

The number of sires (nSires) selected varied among the scenarios (Figure 5A and 5B). For TS (OF1) and TS + FM (OF2) the number of sires selected was constant and equal to 13 along the generation. For OCS and MS scenarios, the nSires selected were increased along the generations and reached the maximum values, 50 sires selected to be mate with 50 females.

4.4. Discussion

As expected, the truncations selection scenarios (OF1 to OF3) were the strategy that provided the highest breeding value (Figure 1A), also presenting an expressive increase in the average coancestry, in comparison to the OCS and MS strategy. The expected consequences of a higher coancestry are the increase of the inbreeding (Figure 3), the reduction of the genetic variability (Figure 2) and the reduction of genetic response in the medium and long-term, and possibly some indirect undesirable responses (Weigel, 2001). However, in truncation selection, the loss of genetic variability do not result in reduction in genetic gain, but the results could be different if the inbreeding depression was considered in the simulation process. In salmonids populations, some studies reported the magnitude of inbreeding depression for harvest weight ranged from -0.6% to -2.6% for each 10% increase in inbreeding (Josefa et al., 2001a, 2001b; Rye and Mao, 1998; Su et al., 1996). Pray and Goodnight (1995) suggested that the decreasing in additive genetic variance is the bottleneck to limit the evolutionary potential of a population. In conservation and breeding programs, for example, the loss of genetic variability results in a reduced population size and the loss of respond to new selective pressures, that may be an important manifestation of inbreeding depression.

A large variation of sires selected for different objective functions was observed (Figure 5A and 5B) and have two effects in this study. The first is related to the powerful of the algorithm in optimize the objective function to find the optimum solution. For example, in truncation selection (OF1) it is possible to guarantee the optimum solution. For this, the optimum number of sires selected must be 13 males with the best true breeding values for mating with 50 females, considering that each male would be mating with until four female. It resulted in selected 12 males used four times and one male used

twice. Therefore, due the stochastic nature of evolutionary algorithms, for objective function that involved some components, as coancestry, inbreeding and progeny variability, an optimum local can be provided instead of the optimum global. The second is related to the coancestry level and selection intensity. The increase number of males selected is the result of higher importance for coancestry in OF5 to OF11. More males selected reduced the coancestry and the inbreeding and, in long-term maintained the genetic gain. In contrast, for truncation selection scenarios, the high selection intensity, the excessive use of the same breeders and the possibility of the best animals selected being relative culmination in higher coancestry and inbreeding levels.

In OCS, firstly the candidates to reproduction are select and the secondly the mates are define (Grundy et al., 2000, 1998; Meuwissen, 1997; Wray and Goddard, 1994). Some studies showed the requirements in applied different mate strategies combined to OCS to constrain the inbreeding levels (Caballero et al., 1996; Carvalheiro et al., 2010a; Skaarud et al., 2011; Sonesson and Meuwissen, 2000). Therefore, our results showed that OCS + RM resulted in a reduction in inbreeding level, compared to truncation selection (Figure 1A), but was evident that the best results depend on how the animals select would be allocate mates, as in OCS + FM and MS scenarios. Minimizing the coancestry using mating strategies generates less inbreeding than random mating, because delays the onset of inbreeding by minimizing the level of inbreeding in the next generation (Caballero et al., 1996; Sonesson and Meuwissen, 2000; Toro and Pérez-Enciso, 1990) and generates lower rates of inbreeding after the onset of inbreeding (Caballero et al., 1996). However, in general, mating designs have received less attention than selection methods, because selection has the largest impact in long-term genetic gain (Henryon et al., 2014). However, choosing appropriate mating designs the genetic gain can increase in long-term and it is possible constrain the coancestry and inbreeding more efficient (Caballero et al., 1996; Henryon et al., 2014, 2009; Sonesson and Meuwissen, 2000).

Alternatively, the MS strategies improves the flexibility and efficiency of the breeding program, because incorporates decisions on animal selection and mate allocation simultaneously, whereas that the best animals to select depends on pattern of mate allocation, and vice versa (Kinghorn and Shepherd, 1999). However, at high

inbreeding rates in long-term, the cost on relationship is low and we observed that the search for optimization of MS scenarios was similar to OCS scenarios. In contrast, as previously stated, the short-term result is in agreement with Yoshida et al. (2017), who also observed evidence that MS outperformed OCS in controlling inbreeding under the same expected genetic gain in the short-term, in a real Nile tilapia and coho salmon datasets. This result highlights that accounting to selection and mate decision simultaneous (MS), and not in two steps (OCS), allows a better control of inbreeding in the short-term. We supposed that with smaller rates of inbreeding the MS algorithm had more opportunities to select and mating the parents that maximize genetic gain and constrain inbreeding, which differ from long-term. Wray & Goddard (1994) suggested that mating designs obviously affect inbreeding in the next generation, but in general they are less important than the selection criterion in controlling long-term response and just a direct constraint on inbreeding cannot effectively control rates of inbreeding.

We tested different weights values for each component of the objective function, but in general there are no rules for choosing the weights. Carvalheiro et al. (2010a) and Wray and Goddard (1994) suggest that the choice of the weights values depends on the time horizon to being considered, the level of reduction in genetic progress in short-term and the average coancestry of current population. Therefore, the optimal weights to be used for the different components of the OF cannot be analytically determined in the evolutionary algorithm implemented. They need to be determined empirically and to overcome this drawback, Yoshida et al. (2017) recommended to run the algorithm several times varying the weights for the different components, explore the potential outcomes and choose the set of weights that would result in a better balance among the different components, according to the goal of the breeding program.

In present study, the results using simulated dataset reinforcement the results found in previous study using real Nile tilapia and coho salmon dataset (Yoshida et al., 2017), that the MS outperformed OCS in short-term. However, using the present simulation dataset, a small different in constrain the inbreeding level between the strategies was found for long-term. A future simulation study testing different structure, for example, applied MS and OCS in a population with a cumulated level of inbreeding could increase

the difference between the strategies. So, in general, the MS was efficient in controlling inbreeding concomitantly to promote genetic progress, furthermore this strategies could implemented in aquaculture breeding programs without extra costs.

4.5 Conclusions

The inbreeding level can be better controlled by MS than by truncation selection and OCS followed by random mating. In the short-term and under the same genetic gain, the MS was more efficient in controlling inbreeding than the OCS followed by minimum inbreeding mating. However, in the long-term, MS and OCS presented similar results regarding the genetic gain and level of inbreeding.

Acknowledgments

GMY acknowledge Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP processes numbers 2014/20626-4 and 2015/25232-7) for Doctoral fellowship. RC acknowledge Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, process number 308636/2014-7) for fellowship.

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