New Zealand aquaculture selective breeding: from theory to industry application for three flagship species

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Summary

Aquaculture is an important primary industry for New Zealand and the three flagship species, Greenshell™ mussels (*Perna canaliculus*), Pacific oysters (*Crassostrea gigas*), and Chinook salmon (*Oncorhynchus tshawytscha*), currently produce over NZD $400 million p.a. in export revenue (www.aquaculture.org.nz). The aquaculture industry has set an ambitious target to increase that revenue to $1 billion p.a. by the year 2025 through a combination of expanding production of these species and developing high value premium markets for added-value products.

The aquaculture industries for all three species began in the 1960-70s, but it was not until the mid-1990s that stock improvement through selective breeding was implemented. The first Chinook salmon family breeding programme was established in 1994 by commercial salmon farming company Southern Ocean Seafood Ltd. The Cawthron Institute initiated a Pacific oyster breeding programme in 1999 using a combination of between- and within-family selection. Later in 2002 Cawthron produced the first Greenshell™ mussel families using wild parents and have since established a family-based breeding programme, now operated and managed by SPATnz and BreedCo Ltd. In 2007, the second largest salmon farming company, Sanford Ltd., decided to move away from mass selection and has since developed a combined between- and within-family selection programme. The breeding programmes for all three species are designed so that the families are evaluated on one or more commercial farms, either in mixed family groups or as separate replicated families.

The initial selection focus was improved growth, and moderate to high heritabilities were estimated for the growth traits in all three species. As a result, time to harvest was significantly reduced. As the industry has developed, more emphasis has been placed on quality and yield traits and the development of multi-trait selection indices. The breeding programmes have also allowed the industry to respond effectively to new challenges, such as the mass mortalities of Pacific oysters, which first occurred in 2010 due to a highly pathogenic variant of the oyster herpes virus (OsHV-1 µvar). Moderate heritability for resilience to the virus in lab and field challenges has led to family selection for this trait and improved survival on the farms. We are now developing genomic resources based on SNP genotyping (genotyping-by-sequencing and SNP chip

approaches) to evaluate the potential benefits of genomic selection in all three species.

Keywords: Families, aquaculture, selection, genomics, gain, benefits, Chinook salmon, shellfish

Introduction

A recent report by FAO (2016) highlighted the important potential of aquaculture to contribute significantly to food security and provide adequate nutrition for a growing global population. Current trends also indicate an increasing demand for high quality seafood from an expanding middle class, as countries like China continue to develop. The global aquaculture industry currently provides over 50% of the world's fish for consumption (FAO, 2016) and this percentage will continue to increase as production from the world's capture fisheries remains static.

Meeting the growing global demand for farmed seafood will require innovation to refine existing aquaculture techniques and to apply new technologies to responsibly expand production and enhance product quality. Selective breeding provides one such technology (Gjedrem *et al*., 2012). With their high fecundity and often shorter life spans than terrestrial livestock, aquatic animals are excellent candidates for selection. Family-based selective breeding programmes for a few key species have demonstrated this potential; the Norwegian Atlantic salmon (*Salmo salar*) breeding programme (Gjedrem, 2010), and the widely disseminated Genetically Improved Farmed Tilapia (GIFT) (*Oreochromis niloticus;* Marjanovic *et al*., 2016).

In the past 40 years aquaculture in New Zealand (NZ) has grown from small beginnings to a significant primary industry. Tonnage is small on a global scale, but the industry has built an international reputation for the supply of high quality seafood to many overseas markets. Demand for NZ farmed seafood currently outstrips production and the industry has a goal to produce higher value branded products to meet domestic and export market demands. Since the early 1990s the industry has recognised the potential gains from selective breeding and the challenge has been to develop programmes that can overcome biological obstacles (such as larval rearing) and operate cost-effectively on a relatively small scale while still providing significant gains.

Current aquaculture breeding programmes in New Zealand

In this paper we describe the history and current status of genetic improvement programmes for the three flagship species, Chinook salmon (*Oncorhynchus tshawytscha*), Greenshell™ mussel (*Perna canaliculus*) and Pacific oyster (*Crassostrea gigas*). We also discuss the benefits these programmes have provided the industry and the potential to enhance these gains through genomic selection. To meet future demands the industry will require continued progress in all sectors of the industry and that must include the implementation of practical methods of genetic improvement.

Chinook salmon

Farming history

NZ is globally the largest producer of farmed Chinook salmon, a Pacific salmon species renowned for its premium flesh quality. Chinook salmon were originally imported to NZ in the early 1900's from the McLeod River, a tributary of the Sacramento River in California (McDowall, 1994). Over the last ≈ 30 generations, evidence suggests that detectable population structure has arisen among these NZ populations (Kinnison *et al*., 2011).

Interest in salmon farming grew steadily in NZ during the 1970s and the first commercial farm was established in 1976 at Waikoropupū Springs in Golden Bay. This was followed in 1983 by the establishment of marine salmon farming in Stewart Island's Big Glory Bay and shortly afterwards in the Marlborough Sounds. Currently, most of NZ's salmon production occurs in sea pens in the Marlborough Sounds or at Stewart Island, with smaller-scale marine production in Akaroa; and freshwater production farms in hydro-canals in the Mackenzie Basin (www.salmon.org.nz). The industry comprises six main companies all based in the South Island; The New Zealand King Salmon Company Limited (NZKS) and Sanford Limited are the two biggest companies. Total production is currently around 12,000 to 14,000 metric tonnes *p.a.* and is predominantly based on the production of all-female stocks (as males have a higher predisposition for early sexual maturation).

Establishing the breeding programmes

The two largest producers, NZKS and Sanford, are vertically integrated companies and operate their own in-house family-based breeding programmes. The first programme was established in 1994 by Southern Ocean Seafood Ltd. From 1996 this programme was continued by NZKS and is now in its eighth generation. In order to establish a broad foundation for future breeding, families were established from 1994 to 1997 with gametes obtained from seven different broodstock sources from around the South Island. Sanford's family breeding programme was established in 2007 and is now in its third generation.

Both programmes now produce ~ 100 to 120 families per year. For the first six generations, the NZKS families were reared to tagging size in individual tanks and fish were subsequently tracked using RFID tags inserted into their body cavity at approximately 10 g live mass. Since 2013, communal family rearing has been incorporated for at least some families from incubation onwards, with the use of microsatellite DNA-based parentage analysis to identify families at harvest, or prior to spawning. More recently SNP-based genotyping has been utilised. This early pooling strategy has also been successfully employed in the Sanford programme.

Commercial trait evaluation

From the outset, sea pen growth performance characterised by weight at harvest was recognised as an important trait for selection, as was age of sexual maturation and fillet colour. To obtain commercially relevant trait data, all-female family smolt are transferred from each year class into a sea pen, and farmed under approximately commercial conditions. Families are harvested before 2 years of age at an average weight of about 3 to 5 kg. More recently, families have been reared over summer for an additional six months to provide summer survival and performance data.

In 1996 and 1997 the first genetic parameters for harvest traits were estimated. These traits included harvest weight, fillet colour, tail fade (colour variation in the tail region of the fillet), body fat, fillet texture and gaping (slits between the muscle blocks) and two year sexual maturation (Symonds *et al*., 2000; Jopson *et al*., 2000). Different methods were also tested for assessing fat (proximate analysis, Distell fish fat meter and X-ray computed tomography) and colour measurement (Roche salmon colour fan, total carotenoid levels and colorimeter). Correlations among the measurements demonstrated colour and fat could be measured using the more cost-effective salmon colour fan and the Distell fish fat meter in future year classes. Heritabilities were also moderate to high for most of the traits measured, suggesting good progress would be made by selection. Favourable (positive) genetic and phenotypic correlations were found between colour and harvest weight. A positive relationship was also found between harvest weight and body fat, and warranted the development of a selection index to avoid the potential for increased fat content.

Additional traits have been analysed in the last five years including spinal curvature using digital X-radiography (Munday *et al*., 2016) and feed conversion efficiency (FCE) (Walker *et al*., 2012). These additional traits have low to moderate heritability, but spinal curvature has been incorporated as a trait in the breeding strategy for one company. FCE is a difficult trait to measure but the benefits could outweigh the costs if FCE can be measured reliably, as feed costs can be as high as 60% of the cost of production.

Breeding objectives and selection strategies

Initially, parents were selected on an index which aimed to maximise growth rate while maintaining quality (fat and colour) at appropriate levels, and minimising losses from early maturity. In some of the breeding programmes selection now also includes body conformation, improved performance and survival over summer. Early maturation at two years is no longer a focus as it is controlled mainly through husbandry and the use of lights in the sea pens.

Estimated breeding values (EBVs) are assessed by best linear unbiased prediction (BLUP) methods based on the selection candidates own records and that of its close relatives (Amer *et al*., 2001). Total genetic merit selection indices are computed using EBVs for each trait and sets of weightings specific to different production systems, and for the breeding nucleus. With the NZKS programme, the final broodstock selection has used an optimisation procedure to balance genetic gain and diversity in the candidate broodstock, but limited to selection candidates that are available for spawning on the day. A combination of among- and within-family selection is applied. Other strategies employed include the use of 2-year-old maturing males from families with an overall low incidence of female early maturation, and the use of cryopreserved sperm from 3-year-old males, a year or more after they spawned. The industry is also developing out of season broodstock through photo-manipulation and high ranking elite broodstock are being used to establish multiplier groups.

Industry benefits

In the 1990s the industry struggled to achieve year round harvests, and salmon growth rate limited production. The selection for faster growth has been very successful, enabling the industry to reliably increase the average weight at harvest year round, thus achieving higher prices in the export market per kg of salmon produced, and providing more consistent supply to domestic retailers. Understanding the favourable and unfavourable correlations among traits has also led to more efficient diet and fillet colour management, and allowed selection for growth to be balanced with body fat content. The genetic gains for growth achieved to date have exceeded the initial expectation of 10% per generation. The NZKS programme has also recently led to the development of a premium quality high value brand, Ōra King salmon (http://orakingsalmon.co.nz), which fetches exceptional prices in overseas markets.

Greenshell mussels™

Farming history

The Greenshell™ mussel (GSM) is endemic to NZ and widely distributed along the coasts of the three main islands (Powell, 1979). Farming of GSM commenced in the 1970's to better manage the production of this species. Farmed mussels are grown to market size on suspended ropes and are of better quality than those harvested from the wild. GSM farming practices have evolved over the years and innovation has allowed the industry to grow and export to over 70 countries, marketed primarily in the form of frozen on the half shell. Annual production ranges from 84,000 to 104,000 metric tonnes and it is the biggest aquaculture industry in NZ based on tonnage and export value (Source: Aquaculture New Zealand).

Until recently the NZ GSM industry depended on wild-caught juveniles (spat) from two main sources: attached to seaweed washed onto Ninety Mile Beach (North Island) or collected using specially designed ropes in Golden Bay and Marlborough Sounds (South Island). These spat supplies are both limited and unpredictable, and the retention of spat on seaweed after translocation to mussel farms is typically less than 5 % (Camara and Symonds, 2014). Farming wild spat precluded genetic improvement of any kind. In 2012 a Primary Growth Partnership (PGP) programme between the industry (Sanford Ltd.) and Ministry for Primary Industries (MPI), led to the creation of Shellfish Production and Technology New Zealand Ltd ($SPAT_{NZ}$) and the development of a world-first purpose built hatchery at the Cawthron Aquaculture Park (CAP) in Nelson for the production of selectively bred GSM spat for commercial production.

Establishing the breeding programme

Producing captive-bred shellfish is challenging due to the potential for high levels of mortality during larval development and was only made effective by the development of a novel rearing system and optimization to enable the simultaneous production of large numbers of families without any significant losses (Ragg *et al*., 2010). The first founder cohort of 75 full-sib families from wild parents was produced in 2002 and another 69 founder families in 2003. Since then over 400 families have been evaluated spanning nine additional cohorts. The families consist mainly of crosses between top-performing families from earlier cohorts, but also include some new wild families and experimental crosses for specific research purposes. 98 families were established in 2017. The breeding programme was originally operated by Cawthron and is now operated by BreedCo Ltd (80% owned by $SPAT_{NZ}$ [a Sanford subsidiary] and 20% by Cawthron).

All families are grown in single-family tanks in the hatchery and nursery (originally at Cawthron and now in the $SPAT_{NZ}$ facility) and allowed to attach onto "family" ropes, which are deployed to sea-based farms, where they are grown until they are large enough to engrave the shell with their family identification number. Commercial evaluation trials are conducted by individually tagging representatives of all families when they reach about 40-50 mm shell length and mixing these marked animals for re-seeding onto rope "droppers" to minimize common environmental effects in the field. These mixed-family droppers are harvested at a standard size of ~ 95mm shell length and destructively sampled to provide family-specific measurements as part of the selection process. Separate, single-family droppers are also held as broodstock. All of the cohorts produced before 2008 were evaluated at a minimum of six commercial farm sites and subsequent cohorts were evaluated at 2-6 sites.

Commercial trait evaluation

Like most aquaculture programmes the initial focus of the breeding programme was on improving growth and meat yield at harvest while maintaining excellent survival and robustness. Over time the range of traits assessed has increased to include: growth rate/size at age, yield (total weight, meat and shell weight), shell dimensions and shape (length, width and height), shell inflation (the ratio of shell depth to shell length), shell breaking strength, meat and gonad condition, food assimilation efficiency, attachment strength and various measures of environmental resilience. Gonad condition (an animal's stage in the reproductive cycle) affects the plumpness and degree to which the meat covers the shell in the frozen product and is, therefore, an important quality-related trait that influences yield and consumer preference.

Analyses of all cohorts produced up to 2014 showed that the heritabilities for key traits are moderate to high (for examples see Camara and Symonds, 2014) and there are no strong adverse genetic correlations between most traits. An exception is shell inflation, meaning that selection for growth using length as the main trait could adversely affect shape if not monitored. While family evaluation across sites identified statistically significant genotype-by-environment (G x E) scaling interactions, family rankings remained relatively stable across test sites. Therefore, multiple GSM breeds are not indicated for the current farm environments and selection traits (BreedCo Ltd unpublished data).

As well as selection for established commercial traits, the programme continues to evaluate additional traits to assess their future potential for selection and to understand the physiological changes in the mussels in response to breeding (Ibarrola *et al*., 2017). For example, live air shipment of GSM to high-value markets represents an opportunity for the industry. Emersion tolerance (survival in air) was recently evaluated in a study with nine families in which variation in family survival was observed (Powell *et al*., 2017). Preliminary analysis also suggests different families have varying resilience to ocean acidification during the fragile early life stages (Ragg, unpublished data).

Breeding objectives and selection strategies

The breeding objectives have evolved to include more traits as more family data have become available. Initially among-family selection consisted of preferentially using families with shell length and meat weight well above average. Within-family selection for shell length was based on informal visual grading of broodstock prior to spawning. Among-family selection is currently based on the family mean of EBVs from a pedigree-based BLUP analysis of the mixed-family dropper data collected at harvest in which multiple core component traits are combined into a selection index. A data analysis pipeline for GSM has been created to both estimate BLUP breeding values using pedigree-based mixed models and balance genetic gain versus the loss of genetic diversity using an optimal contribution approach (Meuwissen & Luo, 1992) implemented in the EVA (EVolutionary Algorithms) software (Berg *et al*., 2006).

Industry benefits

In the 15 years since the first families were established, the GSM breeding programme has gone from theory and proof-of-concept to successful commercial application. Selection response has been positive with improved growth, a reduction in the time to harvest and more consistent product. A commercial breeding company, BreedCo Ltd., in partnership with SPAT$_{NZ}$, now manages the programme and disseminates the gains to industry. Through hatchery innovations within a custom designed facility, elite broodstock can now be reliably spawned for commercial production and new families produced. The advent of hatchery spat production removes the constraint imposed by an uncertain and variable wild spat supply, and unlocks future industry growth. The initial financial benefits are expected to be around $80 million a year by 2026, or up to $200 million per year if the technology is adopted throughout the NZ industry.

Pacific oysters

Farming history

Pacific oysters originating from Japan arrived in NZ in the 1950s. Farming in NZ began in the 1970's and the industry currently produces close to 2,000 tonnes per annum. Pacific oysters are farmed mainly in the North Island and in the Marlborough Sounds. The oyster industry was originally wholly reliant on wild caught spat collected on timber sticks that were subsequently grown on inter-tidal racks on the farms. More recently hatchery capacity developed at Cawthron has led to the production of hatchery reared spat being utilised for production by the largest farming company (Moana New Zealand) and their contract growers.

Industry production peaked in 2009/2010, after which the industry was devastated by mass mortalities caused by a highly pathogenic variant of the oyster herpes virus (OsHV-1 µvar) known to also cause mortalities in oysters overseas (Camara *et al*., 2017). Through changes to husbandry, stock management and selection for survival, the industry is now in recovery and annual tonnages are once again increasing.

Establishing the breeding programme

The Cawthron initiated a family-based breeding programme in 1999 (9 families). The 2001 and 2003 cohorts consisted of 60 families using wild (2001, 2003) or selected (2003) broodstock as parents. The oyster generation time is two years and a total of 9 cohorts have been established, with 80 families set up in 2017. All families are grown in single-family tanks in the hatchery and in the nursery (originally at Cawthron and now in Moana NZ's nursery at CAP) before being transferred in replicated bags to at least two commercial farms in the North Island for evaluation. Broodstock are also reared at commercial sites.

In 2010, the sudden and unanticipated mass mortalities caused by the oyster herpes virus precipitated a shift in the programme's priorities. Cawthron developed upgraded biosecurity systems and procedures and increased surveillance of its broodstock conditioning and hatchery facilities to allow the continued production of selected families. The use of survivors from field trials at OsHV-1 µvar infected farm sites as broodstock was possible, once it was determined that the virus was not transmitted from parents to offspring during strip spawning.

The breeding programme was initially operated by Cawthron, supported by government funding and in collaboration with multiple industry partners, including Aquaculture New Zealand after the virus mortalities in 2010. More recently a commercial breeding programme has been developed with Moana NZ using family broodstock from the 2011, 2013 and 2015 cohorts, selected from their farms and spawned at Cawthron in 2017.

Commercial trait evaluation

Preliminary evaluations found high survival of all 1999 families tested, with large differences in family growth rates and no evidence of strong G×E interactions. From 2003 to 2010, the traits measured were mainly growth (based on length and weight), yield (meat weight, top and bottom shell weight), and aesthetic qualities, such as higher meat volume, desirable shell characteristics (e.g. shape, colour and degree of ridging) and uniformity (King and Janke, 2006).

Following the devastating impact of the OsHV-1 µvar virus, survival became the most important trait and field and laboratory virus challenges were established to evaluate the 2011, 2013 and 2015 families (Camara and Symonds, 2014; Camara *et al*., 2017). Field challenges consisted of rearing families in replicated bags at two known infected farm sites and assessing survival one to three months after the first mortalities occurred. Funding was obtained through Aquaculture New Zealand and MPI to develop a laboratory based OsHV-1 µvar live virus challenge (Camara *et al*., 2017). This challenge was used to evaluate survival in 36 of the 2013 families and 31 of the 2015 families. Data from the 2011, 2013 and 2015 families including harvest traits (2011 and 2013 families) and survival, were combined to estimate genetic parameters using a mixed-model analysis in ASReml.

Shell shape is a key quality attribute and it is important to monitor this trait in order to avoid inadvertent unfavourable changes when selecting for growth. A new approach was used to define the shape traits and two shell shape ratios were expressed as deviations from the ideal shape, rather than the actual ratios (Table 1). What constitutes the "perfect" oyster differs among farmers and the ideal length:width and length:depth ratios were developed through discussions with Moana NZ.

Heritabilities were moderate to high, and sufficient to expect a substantial response to selection (Table 1). A positive genetic correlation between the field and laboratory virus challenges indicated that the laboratory virus challenge is a reasonable proxy for the field virus challenge and is useful for OsHV-1µvar resilience selection. The genetic correlations between traits provided no evidence of genetic trade-offs between survival and quality-related traits.

Table 1. Heritability (± SE) estimates using the combined data from the 2011, 2013 and 2015 Pacific oyster families (2015 families = survival data only).

Trait	Heritability	SE
Field survival	0.304	0.033
Lab survival	0.416	0.072
MeatWt:Shell Volume	0.244	0.064
Length:Width Deviation	0.550	0.094
Length:Depth Deviation	0.471	0.086
Shell Volume	0.413	0.085

Breeding objectives and selection strategies

The breeding objectives of the Pacific oyster breeding programme from 2003 to 2010 were mainly growth and aesthetic qualities, with selection based on family-level phenotypes for semi-quantitative family rankings by panels of producers and processors. After 2010 the objective was to improve resilience to the OsHV-1 µvar virus as rapidly as possible while retaining as much as possible of the genetic gain for quality-related traits achieved during the previous decade of selection. In 2013, the programme transitioned to using pedigree-based mixed-model BLUP to estimate genetic parameters and EBVs using quantitative measurements on individuals. The multi-trait selection index developed for the 2011, 2013 and 2015 families included OsHV-1 µvar resilience (field and lab survival where available), as well as growth, yield and quality traits.

Industry benefits

The oyster family programme has developed from small scale research to a commercial programme utilised by the industry to produce superior farmed product. This is highlighted by the selection for OsHV-1 µvar resilience. The OsHV-1 µvar virus devastated the industry with close to 95 % mortality. Aquaculture New Zealand (http://www.aquaculture.org.nz/) estimated that the value of the industry fell from NZ$ 30 M per year to around NZ$ 15 M per year when the virus emerged, despite a rise in the market price for oysters (Dollimore, 2014). After two generations of selection weighted heavily for survival, mortality is now reported by farmers to be less than 30%. There is still room for improvement but mortality rates are manageable and the industry is once again thriving.

Future opportunities: Genomic selection

Genomic selection can add additional value to aquaculture breeding programmes, especially for high value or difficult to measure traits such as disease resistance, survival and FCE. It also provides an opportunity for much more reliable within-family selection, which can otherwise be difficult to achieve for aquaculture species. The ability to cost-effectively genotype individuals for thousands of SNPs has opened up a significant opportunity for more accurate selection and improved genetic management. For example, families can be pooled during early rearing to avoid the bias due to common environments. AgResearch, Cawthron and the aquaculture industry are working together to assess the feasibility of using genotyping-by-sequencing (GBS) to reliably genotype individuals from the established salmon and GSM breeding programmes for thousands of SNPs. Cawthron are also collaborating with the Roslin Institute in the UK to use their Pacific oyster SNP chip to identify SNPs associated with OsHV-1µvar resilience.

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