Genetic parameters of Greenshell™ mussel traits under two harvest seasons

AS Hess[a*], KG Dodds[a], RD Roberts[b], N King[c], J Symonds[c] and SM Clarke[a]

[a]AgResearch Invermay, Private Bag 50034, Mosgiel 9053, New Zealand; [b]SPATNZ, P.O.Box 10022, The Wood, Nelson 7047, New Zealand; [c]Cawthron Institute, 98 Halifax Street East, Private Bag 2, Nelson 7010, New Zealand

Corresponding Author: Email: andrew.hess@agresearch.co.nz

Abstract

Greenshell™ mussels (GSM) are a mollusc endemic to New Zealand and are of economic importance to the New Zealand aquaculture industry. The primary focus of the GSM industry is selection for increased meat weight, however, aesthetics also influence marketability. This study focused on pedigree-based estimation of heritabilities and genetic correlations among GSM traits collected during two harvest seasons: standard and winter. Sizes and weights were highly heritable (0.41±0.07 to 0.92±0.09), and highly genetically correlated across traits and seasons (≥0.75±0.07). Meat cover and gonad scores (measures of visual appeal) had lower heritabilities than did size and yield traits (0.08±0.03-0.25±0.05). Under standard conditions, meat cover had a high genetic correlation with gonad condition scores (0.85±0.04). Under winter conditions the relationship between meat cover and gonad scores was negative (-0.52±0.19). Substantial GxE was observed across seasons (meat cover: r_g=-0.58±0.16; gonad: r_g=0.62±0.11). Progress made from genetic selection to increase meat yield while controlling for the size may be slow, so selecting for traits related to visual appeal may be preferable. Given that production traits are genetically similar across harvest conditions, selection within standard conditions is likely to improve performance in both standard and winter harvests, thereby allowing for an extended harvest period. However, the genetic improvement of visual appeal of the mussels is likely to be influenced by target harvest season.

Keywords: mussels; heritability; genetic correlations; GxE

Introduction

The Greenshell™ mussel (GSM) is an endemic mollusc of economic importance to the New Zealand aquaculture industry (Camara & Symonds 2014). SPATNZ (www.spatnz.co.nz) runs a Primary Growth Partnership programme (a collaboration between industry and New Zealand's Ministry for Primary Industries) with the aim to produce innovations to advance New Zealand's mussel aquaculture industry and deliver benefits for New Zealand's economy. SPATNZ has been developing techniques for large-scale production and selective breeding to optimise traits for producers and consumers. Typical harvest months for GSM in the main growing area of Marlborough are between October and May. Extension of this harvest season throughout the winter months would have economic benefits to the industry if consumer acceptance remains high in the offseason.

Mussel farming relies on collecting wild spat (baby mussels) from the coast line and transporting them to mussel farms where the spat are subsequently seeded onto rope and grown to a marketable weight. Mature mussels are selected as parents for future generations and selection has focused on size (i.e., length, width, height) and weight (total, shell, and meat) of the individuals. However, traits that influence marketability due to the visual appeal of the mussel to the consumer, are also important.

The aim of this study was to estimate the heritabilities and correlations among size, yield, and traits expected to impact visual appeal in mussels harvested during the standard harvest season or during the winter harvest season. Additionally, genotype by season interactions were assessed within a trait to assess whether these traits were likely to be the same between harvest seasons.

Materials and methods

Animals used

Ethics approval is not required to measure or handle shellfish (http://www.scifair.org.nz/ethics2.html). Data and pedigree information were available on 9,300 2014-born individuals from 83 families (113±30 full-sibs per family) collected at five assessment sites (23±6 full-sibs per site) as part of a growth trial. Individuals were harvested during the standard harvest period (October-March) for four of these assessment sites, while the remaining site was harvested during winter conditions (July). Pedigree information was available on these individuals through a pedigree that included 19,600 individuals.

Phenotypes

Production traits included shell length, width and height, reported in millimetres, as well as meat weight, shell weight and total weight, reported in grams. Two traits were used to assess the visual appeal of the animal: gonad score and meat cover. Gonad score is a visual score of the individual, which considers the size, fullness, and colour of the gonad, ranging from 10 (best) to 1 (worst). Meat cover was defined as the meat weight (expressed in milligrams) per squared millimetre of shell (using the length and width of the individual to calculate the area of an ellipsoid).

Within-season genetic parameters

Variance components were estimated for standard and winter conditions separately in ASReml v4.1 (Gilmour et al., 2015). Heritability estimates were obtained using a univariate model and genetic and phenotypic correlations were estimated using a bivariate model. For individuals collected in standard conditions, the model was:

Y = Site + Animal + Dropper(Site) + e

where Y is the phenotype (or phenotypes in bivariate analyses) described above. Site is the assessment-site code where the mussels were harvested, fitted as a fixed class effect in the model. The random effect of animal was assumed to have a variance–covariance structure proportional to the numerator relationship matrix (A). Additionally, dropper nested within site was fitted as a random effect in the model. Dropper refers to the rope hanging vertically down from a horizontal backbone line on a mussel farm on which the mussels are grown. Approximately thirty animals per family were split across three droppers (10 per family per dropper) separated from one another by ~0.75 m. A similar model was used for variance component estimation under winter harvest conditions, however, due to convergence issues, the random effect of dropper nested within site was dropped from the model. The effect of dropper within site explained a low proportion of the variance (<7±4%) when fitted to the standard dataset and, therefore, will likely have little impact on the interpretation of the results.

Between-season genetic parameters

A bivariate model was fitted considering the traits harvested under the two conditions as separate traits to evaluate whether genotype by environment interactions are likely to be present dependent on which season the animals are harvested in. Because no individuals were grown in both conditions, the residual covariance between the two conditions was set to be zero, and site was fitted as a fixed class effect and Animal as a random effect using the numerator relationship matrix, as described above. An estimated genetic correlation between traits was below 0.8 was considered as evidence for GxE, which was the suggested threshold proposed by Robertson (1959).

Results

Heritabilities

Heritability estimates are shown in Tables 1 and 2 for mussels harvested under normal and winter conditions, respectively. Size-related traits (length, width, and height) and weight-related (total, meat, and shell) traits were estimated to be highly heritable under standard conditions, ranging from 0.51±0.08 for shell height to 0.92±0.09 for shell weight (Table 1). High heritability estimates were obtained for these traits under winter harvest conditions, although the heritability tended to be lower under these conditions, ranging from 0.41±0.07 for meat weight to 0.64±0.09 for shell weight (Table 2). Meat cover and gonad scores tended to be moderately heritable under standard condition (both 0.21±0.04), however, the heritability for meat cover was lower under winter harvest conditions (0.08±0.03).

Correlations between traits

Genetic (below diagonal) and phenotypic correlation estimates are shown in Tables 1 and 2 for mussels harvested under normal and winter conditions, respectively. Size-related traits (length, width, and height) and weight-related (total, meat, and shell) traits were estimated to be highly genetically and phenotypically correlated with each other, with the lowest genetic correlation between these traits under standard conditions estimated to be 0.89±0.03 between shell height and shell width and the lowest phenotypic correlation estimated to be 0.74±0.02 between

Table 1 Heritability (diagonal) and genetic (below diagonal) and phenotypic (above diagonal) correlations during standard harvest seasons.

Trait	Length	Height	Width	Total Weight	Meat Weight	Shell Weight	Meat Cover	Gonad
Length	0.65 (0.09)	0.83 (0.01)	0.90 (0.01)	0.83 (0.02)	0.83 (0.01)	0.91 (0.01)	0.26 (0.03)	0.47 (0.02)
Height	0.90 (0.03)	0.51 (0.08)	0.87 (0.01)	0.83 (0.01)	0.74 (0.02)	0.82 (0.02)	0.24 (0.04)	0.45 (0.03)
Width	0.96 (0.01)	0.89 (0.03)	0.64 (0.08)	0.87 (0.01)	0.78 (0.02)	0.87 (0.01)	0.18 (0.03)	0.44 (0.03)
Total Weight	0.97 (0.01)	0.96 (0.01)	0.95 (0.01)	0.82 (0.09)	0.82 (0.01)	0.98 (0.00)	0.32 (0.03)	0.43 (0.03)
Meat Weight	0.93 (0.02)	0.94 (0.02)	0.90 (0.03)	0.92 (0.02)	0.53 (0.08)	0.82 (0.01)	0.70 (0.02)	0.69 (0.01)
Shell Weight	0.96 (0.01)	0.94 (0.02)	0.94 (0.02)	0.99 (0.00)	0.92 (0.02)	0.92 (0.09)	0.32 (0.03)	0.43 (0.03)
Meat Cover	0.46 (0.12)	0.62 (0.09)	0.37 (0.13)	0.48 (0.11)	0.74 (0.07)	0.48 (0.11)	0.21 (0.04)	0.59 (0.02)
Gonad	0.78 (0.06)	0.78 (0.06)	0.65 (0.08)	0.67 (0.08)	0.89 (0.03)	0.67 (0.08)	0.85 (0.04)	0.21 (0.04)

Table 2 Heritability (diagonal) and genetic (below diagonal) and phenotypic (above diagonal) correlations during winter conditions.

Trait	Length	Height	Width	Total Weight	Meat Weight	Shell Weight	Meat Cover	Gonad
Length	0.53 (0.09)	0.88 (0.01)	0.92 (0.01)	0.89 (0.01)	0.73 (0.02)	0.88 (0.01)	-0.03 (0.03)	0.18 (0.03)
Height	0.89 (0.03)	0.47 (0.08)	0.86 (0.01)	0.86 (0.01)	0.67 (0.02)	0.90 (0.03)	-0.02 (0.03)	0.18 (0.03)
Width	0.93 (0.02)	0.85 (0.04)	0.61 (0.09)	0.88 (0.01)	0.69 (0.02)	0.88 (0.01)	-0.01 (0.03)	0.15 (0.04)
Total Weight	0.92 (0.03)	0.91 (0.03)	0.88 (0.03)	0.59 (0.09)	0.85 (0.01)	0.97 (0.00)	-0.13 (0.03)	0.33 (0.03)
Meat Weight	0.82 (0.05)	0.81 (0.06)	0.75 (0.07)	0.89 (0.03)	0.41 (0.07)	0.71 (0.02)	-0.27 (0.02)	0.60 (0.02)
Shell Weight	0.87 (0.01)	0.90 (0.03)	0.87 (0.04)	0.99 (0.00)	0.80 (0.06)	0.64 (0.09)	-0.06 (0.03)	0.17 (0.04)
Meat Cover	-0.27 (0.20)	-0.35 (0.20)	-0.18 (0.21)	-0.52 (0.17)	-0.65 (0.15)	-0.44 (0.18)	0.08 (0.03)	-0.15 (0.02)
Gonad	0.20 (0.16)	0.31 (0.16)	0.15 (0.16)	0.32 (0.15)	0.66 (0.10)	0.18 (0.16)	-0.52 (0.19)	0.25 (0.05)

Table 3 Raw mean (s.d.) and genetic correlation (s.e.) between normal and winter harvest conditions.

Trait	Normal	Winter	r_g
Length	98.58 (11.59)	100.60 (8.02)	0.99 (0.01)
Height	28.67 (3.43)	28.94 (2.35)	0.99 (0.01)
Width	44.17 (4.57)	44.72 (3.21)	0.98 (0.01)
Total Weight	36.03 (10.30)	32.33 (7.00)	0.99 (0.01)
Meat Weight	12.94 (3.69)	9.61 (2.49)	0.94 (0.02)
Shell Weight	23.09 (7.05)	22.71 (5.05)	0.99 (0.01)
Meat Cover	3.73 (0.65)	2.25 (0.92)	-0.58 (0.16)
Gonad	5.80 (1.38)	2.93 (1.40)	0.62 (0.11)

shell height and meat weight (Table 1). High correlations were also observed between these traits under winter harvest conditions, although the correlations tended to be slightly lower (Table 2).

More variability was observed between visual and production traits both within (Tables 1 and 2) and between conditions (Table 3). Under standard harvest conditions, moderate correlations were observed between meat cover and size and yield traits, with the strongest genetic correlations observed between meat cover and shell height (0.62±0.09) and meat cover and meat weight (0.74±0.07). This trait was also highly correlated with gonad scores (0.85±0.04). Correlations of gonad scores with size and yield traits were high, ranging from 0.65±0.08 (with shell width) and 0.89±0.03 (with meat weight). In mussels harvested under winter conditions, however, the relationships of these traits with size and yield traits, and with each other, substantially changed. Meat cover was estimated to be moderately negatively correlated with size and yield traits, the most negative correlations being observed with total weight (-0.52±0.17) and meat weight (-0.65±0.15). This trait was also negatively correlated with gonad scores (-0.52±0.19). Gonad scores were generally weakly correlated with size and yield traits in mussels harvested under winter conditions, ranging from 0.15±0.16 between gonad scores and width and 0.66±0.10 between gonad scores and meat weight.

Correlations between harvest conditions

Raw means were consistent between standard and winter conditions for production traits but were slightly lower in winter conditions for visual appeal traits (Table 3). For size and yield traits, genetic correlations between harvest conditions were very high, with the lowest estimated correlation between conditions being observed for meat weight (0.94±0.02). Consistent with change in relationships between traits observed in the above analysis, substantial evidence of genotype by environment interactions (GxE) were observed for meat cover, with an estimated genetic correlation between harvest conditions of -0.58±0.16. Although to a lesser extent, evidence for GxE was also found for gonad scores (r_g=0.62±0.11).

Discussion

The Greenshell mussel is the predominant aquaculture species in New Zealand, with sales contributing approximately \$340M to GDP. Selecting on traits collected during mussel harvest, along with recording pedigree information, presents an opportunity to improve economically relevant traits and increase the profitability of this important New Zealand industry. The success of breeding is influenced by the heritability and the variability of the trait. Therefore, providing heritability estimates provides an expectation of the amount of progress that can be made by selection. Limited information is available in the literature about genetic parameters in cultivated mussel species, with the primary body of literature focused on the blue mussel: *Mytilus edulis* or *Mytilus chilensis* (Mallet et al. 1986; Strömgren et al. 1989; Toro et al. 1990; Toro et al. 1991; Toro et al. 1996; Toro et al. 2004; Alcapan et al. 2007). Furthermore, little information is available on the impact of selecting animals in different environmental conditions (e.g., grown in standard industrial conditions or during winter). The ability to extend the harvest season will increase the profitability of the industry if substantial genetic progress can be made that is consistent between these environmental conditions. Therefore, the aim of this study was to estimate and compare the genetic parameters of important GSM traits under standard and winter harvest conditions.

Heritabilities

In general, the heritabilities estimated in this study were high. In aquaculture species, estimates of the heritability of traits tend to be lower in studies that have estimated realized heritabilities through selection experiments (Toro et al. 1990; Toro et al. 1991; Toro et al. 2004; Alcapan et al. 2007) than estimated from fitting standard animal genetic models (Mallet et al. 1986; Strömgren et al. 1989; Toro et al. 1996). The models that fit a standard animal model, while ignoring common environmental variation, are likely to be over-estimating the heritability of the traits (Alcapan et al. 2007). For tracking purposes, the juvenile mussels in our study were raised by family in the same tank until they are mature enough to be placed on the droppers, where they finish growing through to harvest. Thus, a substantial amount of confounding existed between the family (i.e., common environmental term), when also included as a random effect in the model, and animal in our dataset, which presented convergence issues and likely underestimated the genetic component. Thus, the model used in this study to estimate heritabilities excluded the common environmental term and represents the upper bound of heritability in this dataset. Inclusion of more generations of individuals from the same mating pair would help to reduce this confounding and allow us to parse the additive genetic and common environmental terms. Currently, we are also testing use of genomic information as an alternative to pedigree-based methodologies which may afford the ability to better parse out additive genetic variation, non-additive genetic variation, as well as common environmental variation. This approach would also ease the burden of recording pedigree, which is often a painstaking process in this industry.

Genetic correlations

Genetic correlations between size and yield traits were high in both standard and winter conditions. It may be desirable to increase meat yield with minimal increase to shell weight and overall size of the animal. The genetic correlations estimated in this study indicate that progress towards meat weight would be slow if the desire is to constrain the size of the animal.

A crucial aspect of the marketability of the animal is the overall visual appeal of the animal during consumption. In this study, we have included two measurements expected to be related to the visual appeal of the mussel: meat cover and gonad score. Meat cover, calculated as mg of meat/mm^2 of shell (using shell length and width measurements), is a measurement of the overall fullness of the meat within the shell (presentation in the half-shell). Under standard conditions, this was positively correlated with all size and yield traits, with the strongest correlations being observed with meat weight and shell height. The strong correlation of meat cover with shell height suggests this dimension as a limiting factor to meat growth, which is also reflected in the correlation with meat weight. This trait was strongly correlated with gonad score. Gonad score is a visual score that includes the plumpness and colour of the gonad. Thus, it is unsurprising that gonad score is highly correlated with meat cover as well as the size and yield traits.

Unexpectedly, meat cover was negatively correlated with all yield traits and gonad scores under winter conditions. This is likely related to cold stress, lack of available food, or both (McNamara & Buchanan 2005). Studies focused on parasitic infection have shown that feed availability is the primary limiting factor in performance when an individual is faced with pathogen challenge (Doeschl-Wilson et al. 2009; McNamara & Buchanan 2005), with the performance being heavily influence by the individual's ability to grow as well as its ability to fight infection. Previous studies have shown GxE in blue mussels dependent on feed availability at a site (Toro et al. 1996), and this GxE does not appear to be present between sites under normal conditions (Alcapan et al. 2007). We can view the winter harvest period as a period of stress in which, due to limited resource (feed) availability, the energy generated from metabolism of stored energy can be used either for growth and reproduction or to maintain condition (McNamara & Buchanan 2005). Thus, while we do not see much impact in the relationships between size and yield traits, their relationships relative to one another change. This is also reflected in the reduction of the relationships between gonad scores and size and yield traits, which could be viewed as the need of the animal, in some situations, to choose to focus on reproduction or growth. These trade-offs are then reflected in the GxE observed for meat cover and gonad scores.

Conclusions

This study has shown that the expansion of the growing season of GSM is likely to be successful due to similar-sized mussels between normal and winter conditions, however there is a slight decrease in visual appeal for mussels harvested in winter. Mussels grown in winter conditions probably focus limited feed resources to maintenance rather than to growth and reproduction, leading to GxE between the two harvest seasons. It is recommended that selection of mussels take place during the normal season only because most mussels are grown during this season and there is a negative correlation for visual appeal traits between the two seasons. The generally high heritability estimates suggest that selection for these traits will lead to substantial improvements, but the high genetic correlations between yield and size traits indicate that genetic gain will be slow if the goal is to increase meat yield without impacting the size of the individual.

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