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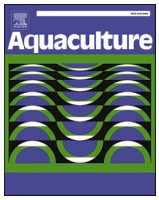

Genetic parameters and genotype by environment interaction in a unique Indonesian hybrid tilapia strain selected for production in brackish water pond culture

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ABSTRACT

Recurrent farming failures due to disease outbreaks have driven Indonesian shrimp farmers to develop co-culture between shrimp and tilapia. For this reason the Research Institute for Fish Breeding (RIFB) Indonesia has started to develop a fast-growing tilapia with good growth over a range of fluctuating salinities in brackish water ponds. A freshwater nucleus and evaluation breeding program is the simplest strategy to implement, but requires knowledge on the extent of genotype by environment (GxE) interaction between fresh and brackish water environments. The objectives of this study were: 1) to investigate the presence of GxE between brackish water and freshwater ponds, 2) to investigate the impact of salinity on genetic parameters, and 3) to investigate gonadal development of tilapia in both environments. We produced 91 fish families and for each family, randomly choose 2 groups of 20 fingerlings for communal grow-out in brackish water at salinity 6 to 25 ppt and freshwater for 120–147 days. We recorded harvest weight (HW) and standard length (L) and calculated daily growth coefficient (DGC), growth rate in length (GR(L)) and condition factor (K) for each fish. Gonadosomatic index and maturation score (0/1) was recorded on 6 fish from each family per environment. We estimated genetic parameters using bivariate animal models in ASReml version 4.1. Results: HW, L, DGC and GR (L) in brackish water were significantly higher than in freshwater. Heritability was moderate for all traits in both environments (0.35–0.50). Genetic correlations between brackish water and freshwater for HW, SL, DGC and GR(L) were 0.65–0.74. Gonad weight for males and females, and gonadosomatic index for females in brackish water were significantly higher than in freshwater ($P < 0.05$). Gonad maturity for both sexes had low heritability in brackish water than in freshwater, (0.12 and 0.04 respectively) with a genetic correlation of 0.47. We conclude that there is substantial GxE interaction for growth between brackish water and freshwater. However, the higher mean growth in brackish water suggests that this is not due to salinity per se, but more likely to other differences between the pond environments. We recommend that a breeding program for salinity tolerant tilapia with a safe, stable, low-risk, and bio-secure fresh water nucleus should incorporate sib information on growth performance in brackish water.

1. Introduction

The Indonesian shrimp industry consists of approximately 65% small-scale farmers who have been abandoning their ponds in many areas due to repeated crop failures, and these reductions in production will likely accelerate as climate change drives significant changes in salinity and sea level rises (Dabbadie et al., 2019; Kalikoski et al., 2018; Maulu et al., 2021). Because shrimp production is the most important aquaculture industry in Indonesia with the highest contribution to the national income (MMAF, 2018), this has important economic and

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societal repercussions.

To address this situation, many shrimp farmers have shifted to a shrimp and tilapia co-culture farming system in brackish water ponds. Most tilapia grow quickly in freshwater, but some species and strains can also be cultivated in brackish water (Cnaani and Hulata, 2011; Stickney, 1986; Suresh and Lin, 1992). In addition, several studies (Ath-thar and Gustiano, 2010; Putra et al., 2013) demonstrated that hybrids and improved strains have higher growth than Nile tilapia in brackish water ponds (Aliah, 2017; Setyawan et al., 2015).

To facilitate this transition, the Research Institute for Fish Breeding (RIFB) has been conducting a small-scale breeding program for salinity tolerant tilapia for four generations. The institute acquired a tilapia strain from a private feed company in 2007 that was thought to be blue tilapia (*Oreochromis aureus*). The founders were spawned for multiplication in early 2008 before the start of the breeding program and named the Sukamandi strain. However, Yu et al. (2022) recently compared the whole genome sequence of this strain to both Nile tilapia (*Oreochromis niloticus*) and blue tilapia and discovered that it is actually a hybrid that is genetically closer to Nile tilapia than to blue tilapia. Signatures of introgression suggest that specific genes related to salinity adaptation (*slc25a24* and *cdhl*) have been introgressed from blue tilapia. We assume that inadvertent mixing between blue tilapia and Nile tilapia occurred between 2008 and 2011 because in subsequent communication with the feed company, they explained that they kept blue tilapia in a separate closed facility. Although this was unintentional, it has apparently contributed to improving salinity tolerance in the Sukamandi strain by introducing favourable genetic variants to the population.

To date, the Research Institute for Fish Breeding's breeding program for salinity tolerant tilapia has been based entirely on mass selection using own performance records of candidates from the Sukamandi strain evaluated in a range of brackish water environments. The average selection response after four generations of phenotypic selection for increased harvest weight after ~120 days of growth is 10.29% for males and 9.29% for females (unpublished results).

The current strategy exposes selection candidates to conditions with poor biosecurity, high mortality losses and associated risks. Many practical challenges such as limited control over environmental conditions and transportation from test sites to the hatchery have also resulted in high risk and costs. An alternative strategy is a nucleus-based breeding program similar (Bentsen and Gjerde, 1994; Olesen et al., 2015), to those previously implemented for other tilapia strains (Omasaki et al., 2017), salmonids (Yáñez et al., 2014), and gilthead seabream (Janssen et al., 2018). This approach maintains all selection candidates in a safe and bio-secure environment that does not represent commercial growing conditions and selects among them using performance information from relatives grown in a production environment using mixed-model BLUP to estimate their breeding values (Trong, 2013).

In this case, the population of selection candidates can be kept in safer and more stable freshwater conditions at the research institute and their progeny and/or sibs can be grown and evaluated in brackish water test locations. Because genotypes may perform differently in the holding vs. testing environments due to genotype by environment interaction (Falconer and Mackay, 1996) the performance of candidates in freshwater may not predict their performance in brackish water. Depending on the strength of GxE, this approach may require predicting the breeding values of candidates based on the performance of their relatives rather than own records. GxE interaction between freshwater and brackish water has been studied previously by Luan et al. (2008), Thodesen et al. (2011) and Thoa et al. (2016) based on the genetic correlation between final weight in different environments using models that treat them as separate traits. Thoa et al. (2016), for example, estimated the genetic correlation between harvest weight in freshwater and brackish water (15–20 ppt salinity) as 0.92 ± 0.04 which suggests that selection based on freshwater performance can transfer 92% of the genetic gain achieved to brackish water performance without evaluating sibs or other relatives in the brackish water environment. If this is also true for the Sukamandi strain, it may not be worthwhile to evaluate sib or progeny performance in brackish water.

The previous focused on final weight, but growth rate during on-growing period is the main priority for fish farmers. Selecting on fast-growth is preferable to selecting on harvest weight because it increases feed efficiency, which further contributes to profitability and sustainability of production (Aubin et al., 2009; Besson et al., 2016; de Verdal et al., 2018). However, the genetic correlations between final weight and growth rate were >0.97 (de Oliveira et al., 2016). Consequently, selection for harvest weight within a batch of selection candidates will improve growth rate as a correlated response. In this study, we directly quantify growth rate, which can be expressed as absolute or specific growth rate (Hopkins, 1992), thermal growth coefficient (Jobling, 2003) or daily growth coefficient (Cho, 1992). We expected that higher salinity would reduce growth rates and the expression of genetic variation resulting in lower genetic variance as well as re-ranking of candidates (GxE) between brackish water and freshwater. We also address the implications of GxE for breeding program to improve growth of tilapia in brackish water.

Selection for improved performance in brackish water also raises concerns about the potential for increased reproduction and higher probability that escapees may become invasive in estuarine ecosystems via correlated responses to selection. Therefore, we would ideally select for fast-growth, but lower reproduction performance in brackish water without compromising reproductive performance in the freshwater nucleus. This requires further knowledge on the correlation structure between growth and reproduction in both fresh and brackish water.

2. Materials and methods

2.1. Selected parents

We produced our experimental fish using the 4th generation of the Sukamandi strain as selected parents at the Research Institute for Fish Breeding, Indonesia. We maintained the parents in separate 15 m^2 hapas (5 × 3 m), cage-like, rectangular nets with a mesh size of 5 mm suspended in 2000 m^2 freshwater ponds in single sex groups. They were fed twice a day on a commercial pelleted feed with approximately 30% crude protein and 5% fat, at a daily feeding rate of 3% of biomass for four weeks.

2.2. Family production

We produced full- and half-sib families in 65 smaller breeding hapas (4 m^2; 2 × 2 m), suspended in three 200 m^2 earthen ponds at the Research Institute for Fish Breeding. Each of these hapas was stocked with one male and three females by introducing the males to the hapas 1 day before the 3 females. Because tilapia are mouth-breeders in which the female keeps fertilized eggs in her mouth until hatching, and there was only one male in each breeding hapa, this method produces full-sib families from each mated female and paternal half-sib families if a male mates with multiple females.

We conducted this mating process in 7 day cycles, and if none of the females produced eggs during a cycle, we replaced the male. We replaced the male in every hapa after 2 cycles, and replaced spawned females with new females. At the end of each cycle, we collected the fertilized eggs or hatchling/swim-up fry from the females' mouths, recorded her unique identification tag number, and subsequently incubated the eggs from each female in a single cone-shaped hatching jar (25 cm diameter and 40 cm height) with a constant flow of water until they hatched and grew into functional hatchling/ swim-up fry. We labelled the cone based on the female ID and recorded the collection date of eggs or larva and the male parent for each female's progeny. During this incubation period, we removed dead eggs and fry daily. We also stabilised the water temperature during incubation between 28 °C and 30 °C with aquarium water heaters.

In total, we produced 91 families over a period of 105 days (from 21 May to 22 August 2019) consisted of 53 full sib families and 38 paternal half-sib families. In order to facilitate the next steps of the experiment, we divided the resulting families into three batches based on the spawning date. We labelled the first 35 full-sib families from the first four weeks of the reproduction period as batch 1, the next 27 families as batch 2, and the last 29 families as batch 3.

2.3. Fingerling nursery rearing and tagging

Fry hatched after about 5–7 days. After yolk-sac absorption, we transferred swim-up fry from each family into 4 m^2 nursery hapas (2 × 2, mesh size 1 mm) suspended in a 2000 m^2 earthen pond. For this, we randomly sub-sampled 200 fry and stocked them into a single nursery hapa, equivalent to a nursing density of 50 fish per m2. During this period, we fed them twice daily using a commercial powder feed with a dietary protein level of 30%, at the rate of 10–15% of their body weight during the first 3 to 4 weeks. The second nursery period continued until tagging at an average bodyweight of 16 g during which we fed the fingerlings a commercial pelleted feed consisting of 30% protein twice daily at the rate of 10% of total body weight. This nursery period of separate family rearing in nursery hapas ranged from 120 to 161 days. At the end of this period, we randomly chose and tagged 40 individuals from each family using PIT (Passive Integrated Transponder) tags and recorded their identification number, stocking weight (SW) and standard length (L0).

A total 20 fingerlings per family were grown in brackish water and another 20 in freshwater. For logistical reasons, we tagged the fish for brackish water grow out first. The first batch of 35 families were tagged at an average age of 142 days for brackish water grow out and 148 days for freshwater grow out (127 to 161 days of age post-hatching interval) as summarized in Table 1. We tagged the second batch at the average age 134 and 141 days for brackish water and freshwater respectively (123 to 161 days of age post-hatching interval), and the third batch at the average age of 139 for brackish water and 142 for freshwater (128 to 151 days of age post-hatching interval). We then pooled all tagged fingerlings within a batch and water treatment after 3 days of conditioning in fiberglass tanks with minimum feeding rate of 1–3% body weight.

2.4. Testing environments

The test location for brackish water was at the Technical Implementation Unit for Brackish water Culture Karawang (−6.106192, 107.428710), at salinity around 20 ppt, and the location for freshwater/nucleus was at Research Institute for Fish Breeding (−6.371860, 107.623815). Both locations are in the West Java area close to the North Java Sea.

We stocked the tagged and mixed fingerlings from each batch of families in separate ponds on each site at an initial stocking density of ~5 fish per m^2. To minimize stress and mortality during the stocking process, prior to stocking the brackish water ponds we temporarily reduced their salinity level from ~20 ppt to 10 ppt s by reducing the water level and re-filling the pond with freshwater from the irrigation waterway. During the grow out period, we fed the fish twice daily between 07:00 and 09:00 in the morning and between 15:00 and 17:00 in the afternoon with a commercial pellet diet containing 28% protein at a rate of 3–5% bodyweight. We also recorded water parameters such as dissolved oxygen, pH, temperature, and salinity daily using digital water quality tester.

2.5. Trait measurements

Following a grow-out period of 150 to 210 days, we harvested the fish, initially using three drags of a seine net, after which we drained the pond to catch all the remaining fish. We transferred all caught fish directly into a plastic container with diameter around 80 cm containing clove oil (~0.4 ml per litre of water) as an anaesthetic agent. This process was performed to avoid fish mortality due to handling stress during catching and measuring the phenotypic traits. The number of surviving fish at harvest ranged from 3 to 19 fish/family in brackish water and from 1 to 20 fish/family in freshwater (72.9 ± 16.6% in brackish water and 77.1 ± 19.6% in freshwater). During measurements, we weighed each fish for harvest weight (HW) using a digital scale to the nearest to 0.1 g. We also measured the standard length (L) with a ruler to the nearest 1 mm.

From the individual stocking and harvest weights, we calculated daily growth coefficients (DGC, (Bureau et al., 2000)) as:

$$DGC = \frac{HW^{\frac{1}{3}} - SW^{\frac{1}{3}}}{growing\ days}\ x\ 100$$

where *SW* is body weight at stocking, *HW* is harvest weight, and *growing days* is the growing time between stocking and harvest.

Similarly, we calculated individual growth rate for length, GR(L), as:

$$GR(L) = \frac{SL_f - SL_0}{growing\ days}$$

where SL_0 is standard length at stocking, SL_f is standard length at harvest, and growing days is the growing time between stocking and harvest.

We calculated the condition factor (*K*) according to Weatherley et al. (1987):

$$K = \frac{HW}{L^3} \times 10^5$$

with *HW* in grams and *L* in mm

For reproductive performance, we measured gonad weight and maturation stage for 6 fish per family in each environment. We measured gonad weight with digital scale (0.01 g), and macroscopically determined the maturation score (MS) based on Legendre and Ecoutin (1989) with three stages for males and five stages for females. Gonadosomatic index (GSI) was determined as:

$$GSI = \frac{Gonad\ weight}{Body\ weight} \times 100$$

We analysed gonad weight and gonadosomatic index separately for

Table 1
Total number of families, range (mean) of stocking age and harvesting age and rearing period in days, stocked number and harvested number of fish in brackish water (B) and freshwater (F).

Batch	Environment	Number of families	Stocking age	Harvest age	Number stocked	Number harvested	Rearing period
1	B	35	127–155 (142.6)	253–281 (268.6)	640	511	126
	F	35	133–161 (148.6)	258–286 (273.6)	649	482	125
2	B	27	123–154 (134.9)	243–274 (254.9)	489	348	120
	F	27	130–161 (141.9)	270–301 (281.9)	488	425	140
3	B	29	128–148 (139.4)	250–270 (261.4)	568	449	122
	F	29	131–151 (142.4)	278–298 (289.4)	574	484	147
All	B	91	123–155	243–274	1697	1308	120–126
	F	91	130–161	258–298	1711	1391	125–147

each sex because the differences of the scores between sexes was significant.

2.6. Data analysis

2.6.1. Descriptive statistics

We prepared and checked the raw data recorded in Microsoft Excel using R version 4.1 (R-Core-Team, 2021). In total, we obtained data for 1308 fish in brackish water and 1391 in freshwater ponds from 91 families (Table 1). We estimated descriptive statistics and checked for data anomalies using R version 4.1. We performed student *t*-test to evaluate whether HW, L, DGC, GR (L), K, and GW differed between environments.

2.6.2. Phenotypic and genetic parameters

We estimated genetic parameters for performance traits using a total of 2699 individual fish for HW, L, DGC, GR (L) and K. The animal model included fixed effects for pond, sex within pond and harvest age within pond for HW and L. Sex was coded as male (m) and female (f) and harvest age was calculated as the number of days between the stocking date and harvest date. We nested sex within ponds to take into account differences in age and sexual maturity of the different groups of families by estimating different effects of sex in each of the ponds.

We estimated the genetic correlations between environments using a bivariate animal model in ASReml version 4.1 (Gilmour et al., 2015) that treats growth traits in different environments as different traits:

$$y_{ijkl} = \mu + \mathrm{POND}_i + \mathrm{SEX\ (POND)}_{i,j} + \mathrm{AGE\ (POND)}_{i,k} + \mathrm{INIT} + \mathrm{a}_l + \mathrm{e}_{ijkl}$$

where: y_{ijkl} is vector of single growth trait in fresh and brackish water; μ is overall mean; POND_i is fixed effect that accounts for both pond and batch effects ($i = 1$–3 for BW, and 4–6 for FW); $\mathrm{SEX\ (POND)}_{i,j}$ is the fixed effect of sex nested within pond (j = m, f); $\mathrm{AGE\ (POND)}_{i,k}$ is harvest age nested within pond; INIT is initial weight for DGC, initial length for GR and the ratio of initial weight and initial length for K which were standardized by scaling it to a standard normal distribution; a_l is the random additive genetic effect of the l-th individual; e_{ijkl} is random residual effect associated with an individual.

Common environmental effects (c^2) were expected in this study because families were reared separately in family-specific hatching jars and nursing hapas until tagging. However, solutions for c^2 could not be obtained because family effects are confounded with dam effects because our breeding strategy produced very few half-sib families and we had only shallow pedigree information. We tried to fit models that included c^2, but they did not converge. Without the common environmental effect in the model, the solutions converged and the genetic correlations could be estimated. The full model was used to analyse the DGC, GR (L) and K. A simplified model that excluded the fixed effect for initial value (INIT) was used for HW and L.

We calculated the heritability as the ratio between additive genetic variance (σ^2_A) and phenotypic variance (σ^2_P), $\frac{\sigma^2_A}{\sigma^2_P}$. Genetic and phenotypic correlations between different traits in the same environment were also obtained from bivariate analyses. The animal effects were distributed as N(0,A $\otimes$ G) with the additive genetic variance covariance matrix (G) is $\begin{bmatrix} \sigma^2_{A,1} & r_{A,12}\sigma_{A,1}\sigma_{A,2} \\ r_{A,12}\sigma_{A,1}\sigma_{A,2} & \sigma^2_{A,2} \end{bmatrix}$ where $\sigma^2_{A,\ 1}$ ($\sigma^2_{A,\ 2}$) is the additive genetic variance of trait 1 (trait 2), and $r_{A,\ 12}\sigma_{A,\ 1}\sigma_{A,\ 2}$ is the additive genetic covariance between trait 1 and trait 2. The residuals were distributed as N(0, I $\otimes$ R) with residual variance-covariance matrix (R) is $\begin{bmatrix} \sigma^2_{e,1} & r_{e,12}\sigma_{e,1}\sigma_{e,2} \\ r_{e,12}\sigma_{e,1}\sigma_{e,2} & \sigma^2_{e,2} \end{bmatrix}$ where $\sigma^2_{e,\ 1}$ ($\sigma^2_{e,\ 2}$) is the residual variance of trait 1 (trait 2), and $r_{e,\ 12}\sigma_{e,\ 1}\sigma_{e,\ 2}$ is the residual covariance between trait 1 and trait 2. Genetic and phenotypic correlations among traits were calculated as the covariance divided by the product of the standard deviations of the two traits in the bivariate model.

For reproductive performance, we also estimated the genetic parameters with bivariate animal models that take into account the fixed effects of pond and harvest age. For genetic analysis of gonad maturity, we reclassified the maturity score as mature (1) and immature (0) according to Legendre and Ecoutin (1989). We classified females as immature when they were in stage 1 to 3, and as mature when they were in stage 4 and 5. Whereas for males, they were classified as mature when they were in stage 2 to 3. Then we analysed males and females together with sex nested within pond as a fixed effect.

We estimated the genetic correlation between the same traits measured on different (related) individuals in the brackish and freshwater ponds with the bivariate model above. For this model, the additive genetic variance-covariance matrix is $\begin{bmatrix} \sigma^2_{A,B} & r_{A,BF}\sigma_{A,B}\sigma_{A,F} \\ r_{A,BF}\sigma_{A,B}\sigma_{A,F} & \sigma^2_{A,F} \end{bmatrix}$ where $\sigma^2_{A,\ B}$ is the additive genetic variance for the traits in brackish water, $\sigma^2_{A,\ F}$ is the additive genetic variance for the traits in freshwater and $r_{A,\ BF}$ is the additive genetic correlation between brackish water and freshwater.

The covariances of residuals between environments was set to zero, as individual fish were evaluated in only one environment. Consequently, the residual variance-covariance matrix is $\begin{bmatrix} \sigma^2_{e,B} & 0 \\ 0 & \sigma^2_{e,F} \end{bmatrix}$ where $\sigma^2_{e,\ B}$ is the residual variance for the trait in brackish water and $\sigma^2_{e,\ F}$ is the residual variance for the trait in freshwater.

3. Results

3.1. Descriptive statistics

The average salinity, morning and afternoon water temperature in the brackish water pond were 16.21 ppt, 29.57 °C and 33.71 °C, respectively. The salinity in the brackish water was highly variable, fluctuating over time between 6 and 25 ppt as shown in Fig. 1. The lowest salinity was 6 ppt which occurred in raining period. The temperature profiles for the brackish and freshwater ponds are very similar (Fig. 1).

Grow out in brackish water pond resulted in 77.08% survival, and we recovered 1308 out of 1697 fish at harvest time after 120–126 days rearing period. In the freshwater pond, we observed higher survival of 81.82% or 1391 out of 1700 fish after 125–147 days rearing period. Descriptive statistics of *SW, HW, L, DGC, GR, K* and survival are shown in Table 2. The average stocking weight is similar between brackish water (16.11 ± 7.79 g) and freshwater (15.65 ± 7.75 g). *HW, L, DGC* and *GR* were higher for males compared to females in both brackish water and freshwater, but *K* was similar. However, the coefficient of variation for females was higher than males for all growth traits in both brackish water and freshwater. At harvest time, *HW* and *L* were higher in brackish water and significantly different ($P < 0.05$) compared to freshwater. *DGC* in brackish water was higher (3.38 ± 0.43) and significantly different ($P < 0.05$) compared to freshwater (2.72 ± 0.44). In brackish water, *GR(L)* during grow-out period was significantly higher compared to freshwater ($P < 0.05$). The difference between K in brackish water (4.02 ± 0.37) and in fresh water (3.98 ± 0.36) was not significant. The regression coefficients and intercepts of log(*HW*) against log(*L*), were similar in brackish water and freshwater (Fig. 2). Overall, brackish water leads to higher *HW, L, DGC, GR (L)* compared to freshwater.

We evaluated the reproductive performance of males and females in both environments. Macroscopic analysis of gonad weight (Table 3) showed that gonad weight for both males and females and gonadosomatic index for females in brackish water was higher than in freshwater ($P < 0.05$), but for males the difference in gonadosomatic index between brackish water and freshwater was not significant ($P > 0.05$). Gonad

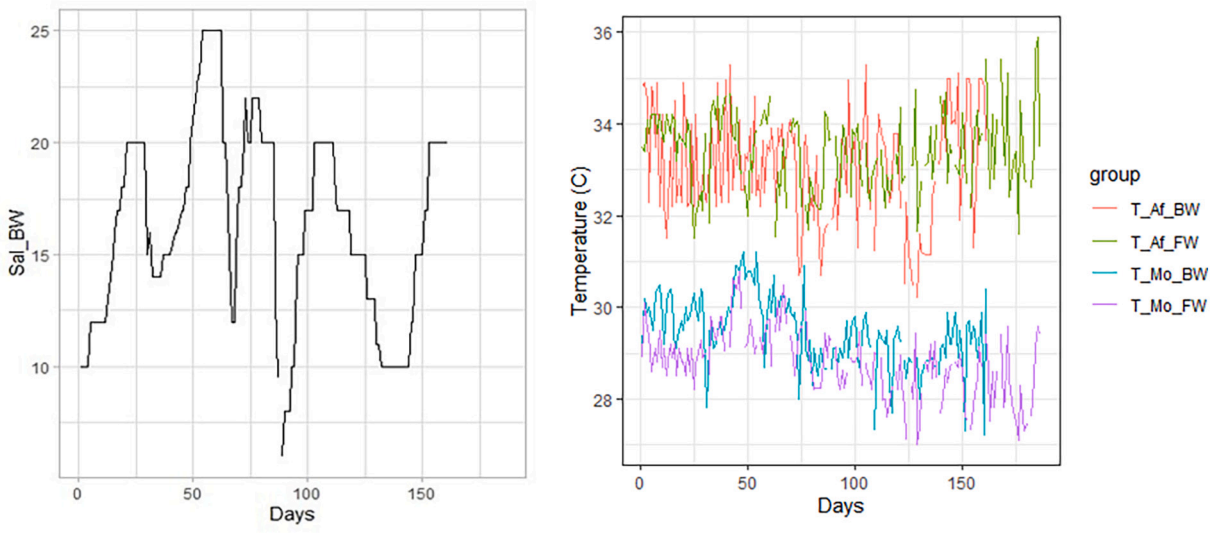

Fig. 1. Daily salinity fluctuation in the brackish pond (left) and temperature (right) in the freshwater pond in the morning (T_Mo_FW) and afternoon (T_Af_FW), and in the brackish water pond in the morning (T_Mo_BW) and afternoon (T_Af_BW) during the experimental rearing period.

Table 2
Number of observations (n), mean and coefficient of variation (CV in %) for stocking weight (SW) and harvest weight (HW), standard length (L), daily growth coefficient (DGC), growth rate (GR (L)), condition factor (K) and survival rate (S) of male and female *Oreochromis niloticus* in brackish water and freshwater.

Trait	Brackish water					Freshwater				
	n	Male		Female		n	Male		Female	
		Mean	CV	Mean	CV		Mean	CV	Mean	CV
SW (g)	1697	16.8 ± 7.49	44.58	16.1 ± 8.60	53.27	1711	15.8 ± 7.28	46.07	15.1 ± 8.06	53.40
HW (g)	1308	324.7 ± 61.43*	18.92	255.0 ± 53.85*	21.14	1391	261.5 ± 49.72*	19.01	201.7 ± 46.60*	23.10
L (cm)	1308	19.9 ± 1.32*	6.63	18.5 ± 1.32*	7.12	1391	18.7 ± 1.20*	6.45	17.1 ± 1.30*	7.62
DGC ($g^{1/3}$ /day)	1308	3.5 ± 0.38*	11.02	3.12 ± 0.40*	12.42	1391	2.84 ± 0.39*	13.81	2.5 ± 0.45*	18.01
GR (L) (cm/day)	1308	0.10 ± 0.011*	10.75	0.09 ± 0.011*	11.74	1391	0.08 ± 0.017*	21.68	0.07 ± 0.012*	17.39
K	1308	3.95 ± 0.38		4.05 ± 0.36		1391	3.98 ± 0.35		3.98 ± 0.36	
S (%)		(77.07)					(81.29)			

* $p < 0.05$ Student-t-test comparing brackish and freshwater ponds.

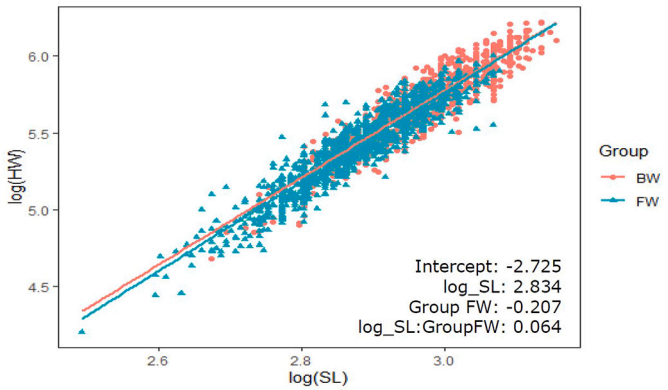

Fig. 2. Log_{10}(HW) plotted against Log_{10}(L) in brackish water and freshwater ponds. HW = harvest weight, L = length.

maturity score varies between sexes and environments (Table 4).

We evaluated the regression coefficience between log(HW) and log (SL) in fresh and brackish water using a separate slopes analysis of covariance (Fig. 2). The estimated regression coefficients in brackish water and freshwater are 2.834 and 2.898, respectively, and are not significantly different (Interaction $p > 0.05$, Table 5). However, the intercept in brackish water was significantly higher than in freshwater (Group effect $p < 0.05$, Table 5).

Table 3
Means ($\bar{x}$), standard deviations (σ), coefficients of variation (CV in %) of gonad weight and GSI male and female from brackish water and freshwater.

Traits	n	Brackish water			n	Freshwater		
		$\bar{x}$	σ	CV		$\bar{x}$	σ	CV
Gonad weight male (g)	299	1.03*	1.50	145.1	280	0.70*	0.76	109.7
Gonad weight female (g)	177	4.52*	3.56	78.6	198	2.42*	2.16	89.2
GSI male	299	0.31	0.50	159.7	280	0.28	0.31	111.1
GSI female	177	1.82*	1.40	77.2	198	1.26*	1.54	91.2

* $p < 0.05$ Student-*t*-test comparing brackish and freshwater ponds.

Table 4
Gonad maturity score (MS) for males and females in brackish water and freshwater.

Male			Female		
Stage	Brackish water	Freshwater	Stage	Brackish water	Freshwater
1	13 (4%)	8 (3%)	1	3 (2%)	2 (1%)
2	39 (13%)	57 (21%)	2	37 (20%)	47 (23%)
3	248 (83%)	212 (77%)	3	56 (30%)	67 (33%)
			4	72 (38%)	66 (33%)
			5	19 (10%)	20 (10%)

Table 5
Separate slopes analysis of covariance for the relationship between standard length (SL) and harvest weight (HW) brackish and freshwater ponds.

Source	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Log_SL	1	179.36	179.36	21,903.095	2e-16
Group	1	0.20	0.20	24.108	9.66e-07
Interaction	1	0.02	0.02	2.129	0.145
Residuals	2686	22.00	0.01		

3.2. Genetic parameters of traits within environments

Genetic and phenotyping variances estimates for all traits in freshwater were lower compared to brackish water, except standard length (Table 6). The h^2 estimates for HW, L, DGC, GR (L) and K were moderate, from 0.35 to 0.50 with small standard error ranging from 0.06 to 0.09. All h^2 estimates for HW and L were higher in freshwater ponds compared to brackish water pond while for the ratio traits (DGC, GR (L) and K), h^2 estimates were higher in the brackish water pond compared to the freshwater pond. We estimated the genetic parameters for reproduction traits separately for the sexes in both environment as shown in Table 7. The h^2 estimates varies from low to moderate (0.03–0.54). The genetic correlation of GW in both environments was higher in male (0.85) than in female (0.50). Genetic correlations for reproductive traits had higher standard errors than growth traits due to the smaller sample size (6 fish/family rather than ~20).

The genetic correlations (r_g) between HW, L, DGC, and GR(L) within an environment (brackish or freshwater) were high (Supplementary Table S1), varying from 0.81 to 0.99 and from 0.79 to 0.99, respectively. Similar trends appear in the phenotypic correlations (r_p). The estimated r_p were high in both environment from 0.86 to 0.99, except for r_p between GR(L) and HW in freshwater which was very high, and the software generated an estimated value >1 (Supplementary Table S2). The r_p and r_g between GR(L) and HW in freshwater could not be estimated due to model convergence problems.

3.3. Genotype by environment interactions

The genetic correlations between brackish water and freshwater for HW, L, DGC and GR (L) were moderate ranging from 0.65 to 0.74. Fig. 3 shows the patterns of the re-ranking of the parents of all families between brackish water and freshwater for DGC based on their estimated breeding values. The DGC interaction plot has many crossings and more families switch rank between environments resulting in lower genetic correlation than other traits. There are crossovers of high-ranking parents between the two environments, indicating that these families will perform differently in both environments. Genetic correlations for reproductive traits (GW, GSI and MS) show high variation between 0.47 and 0.85 with very high standard error (Table 7).

Table 7
Heritability (h^2) and genetic correlation (r_g) for gonad weight (GW), gonadosomatic index (GSI) and Maturity score (MS) in brackish and freshwater and their standard errors (*se*).

Trait	Sexes	h^2(*se*) Brackish water	h^2(*se*) Freshwater	r_g(*se*)
GW	Male	0.13 (0.13)	0.38 (0.14)	0.85 (0.45)
	Female	0.30 (0.17)	0.21 (0.17)	0.50 (0.46)
GSI	Male	0.06 (0.11)	0.54 (0.14)	0.75 (0.74)
	Female	0.30 (0.16)	0.03 (0.15)	–
MS	Both sexes	0.12 (0.07)	0.04(0.07)	0.47 (0.74)

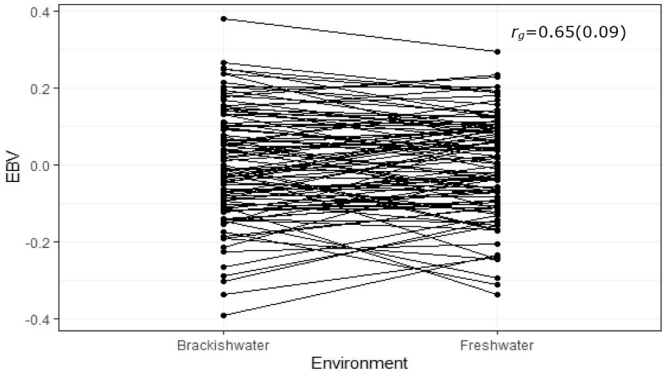

Fig. 3. Reranking of parental estimated breeding valued (EBV) for daily growth coefficient (DGC) between brackish water and freshwater ponds. The genetic correlations (r_g) with standard error are included inside the plot.

4. Discussion

The objectives of our study were to investigate the extent of GxE interactions for growth and reproductive traits between brackish and freshwater ponds in the Indonesian Sukamandi tilapia strain being selected for improved salinity tolerance. This information will be important for redesigning and refining the breeding program. In the next three sections, we discuss the performance of the Sukamandi strain in brackish water, potential for further improvement of this strain and the implications for the (re)design of the selective breeding program.

Table 6
Additive genetic variance (σ^2_A), total phenotypic variance (σ^2_P), heritability (h^2), genetic correlation (r_g), phenotypic correlation (r_p), and their standard errors (*se*) and genetic coefficient of variation (GCV) from bivariate analysis for harvest weight (HW), standard length (L), daily growth coefficient (DGC), growth rate (GR (L)) and condition factor (K) in brackish water and freshwater ponds.

Trait	Brackish water				Freshwater					
	σ^2_A	σ^2_P	h^2(*se*)	GCV[a]	σ^2_A	σ^2_P	h^2(*se*)	GCV[a]	r_g	r_p
HW	1048.47 (222.13)	2958.8 (143.58)	0.35 (0.06)	10.2	790.57 (162.67)	2104.7 (102.22)	0.38 (0.06)	5.2	0.66 (0.10)	0.24 (0.05)
L	0.48 (0.09)	1.24 (0.06)	0.39 (0.07)	3.2	0.53 (0.10)	1.30 (0.06)	0.41 (0.07)	2.7	0.73 (0.09)	0.29 (0.06)
DGC	0.47×10^{-01} (0.97×10^{-02})	0.11 (0.58×10^{-02})	0.43 (0.07)	6.5	0.37×10^{-01} (0.74×10^{-02})	0.09 (0.45×10^{-02})	0.42 (0.06)	3.7	0.65 (0.09)	0.28 (0.06)
GR (L)	0.30×10^{-04} (0.84×10^{-05})	0.73×10^{-04} (0.47×10^{-05})	0.42 (0.09)	4.5	0.26×10^{-04} (0.67×10^{-05})	0.65×10^{-04} (0.39×10^{-05})	0.39 (0.08)	2.8	0.74 (0.31)	0.30 (0.09)
K	0.56×10^{-01} (0.11×10^{-01})	0.11 (0.62×10^{-02})	0.50 (0.07)	5.3	0.54×10^{-01} (0.11×10^{-01})	0.122 (0.63×10^{-02})	0.44 (0.07)	5.2	0.83 (0.06)	0.34 (0.06)

[a] GCV was calculated as: $\left(\frac{\sigma_A}{\mu}\right)$ x 100%.

4.1. The Sukamandi strain performance in brackish water

The Sukamandi strain grew better in brackish water ponds than in freshwater ponds. At ~16.2 ppt HW, DGC, L and GR (L) were significantly higher in brackish water than in freshwater. Because physiological adaptation to elevated salinity requires energy to maintain osmotic homeostasis (Kültz, 2015) and the diverted energy to osmoregulation should reduce growth (Boeuf and Payan, 2001; Tseng and Hwang, 2008), we expected the opposite result based on previous studies of Nile tilapia, which has lower performance in brackish water than in freshwater ponds (Cnaani and Hulata, 2011; Fineman-Kalio, 2008; Kamal and Mair, 2005). The energetic requirements for osmoregulation to depend on the environment, and both hypo- hyper-osmotic conditions require energy to maintain internal homeostasis. Consequently, the best growth performance of tilapia is achieved when they are in isosmotic conditions. Blue tilapia (*O. aureus*) and Mozambique tilapia (*O. mossambicus*) have higher salinity tolerance than Nile tilapia and grow well in brackish water ponds up to 20 ppt for blue tilapia and close to full-strength seawater for Mozambique tilapia (Popma and Masser, 1999). Blue tilapia is in isosmotic conditions at salinities of 8 to 12 ppt based on blood chemistry (Semra et al., 2013). A molobicus hybrid tilapia strain has a salinity tolerance close to *O. mossambicus* (Mateo et al., 2004) and can reproduce in brackish water (Cnaani and Hulata, 2011). Our test condition were at salinity range around 16 ppt, which is closer to the isosmotic condition than freshwater. Our results indicate that the salinity tolerance of the Sukamandi strain (*Oreochromis* spp.) is closer to that of blue tilapia, than of Nile tilapia, most likely because this strain is a unique composite strain of Nile tilapia with introgressed salinity tolerance genes from blue tilapia (Yu et al., 2022). In addition, the strain has been selected for growth and survival in brackish water ponds for 4 generations, prior to the current experiment.

Our expectation was that fish would grow less in brackish water and have lower fecundity. However, we observed higher mean growth in brackish water, compared to freshwater, while gonadal development and maturation was comparable in both environments. The survival rate in brackish water (77%) was close to survival rate in freshwater (81%) which also indicates that the Sukamandi strain has a good salinity tolerance. The regression coefficient between HW and L in Fig. 2 indicate whether fish grow thicker or thinner at the same length. When the slope below 3.0 indicates that fish become leaner and when the slope exceeds 3.0 indicates fish become fatter (Silva et al., 2015). In our study, the regression coefficients are 2.834 for brackish water and 2.898 for freshwater. They are statistically equal as indicated by the non-significant interaction effect ($p > 0.05$) and close to 3, indicating that the fish were in a good condition in both environments. However, brackish water ponds provided a better environment for fish growth than freshwater ponds as indicated by the significant main effect of group ($p < 0.05$). This suggests that salinity itself had no negative effects but that other aspects of the brackish water environment were biologically different and more beneficial for growth than the freshwater pond. A study by Dewi et al. (2012), found abundant phytoplankton and zooplankton, particularly *Calanus* sp. and *Acartia* sp. in brackish water ponds at 95,570 ind./L and 17,120 ind./L far higher than in freshwater ponds at RIFB at 604 ind/L for *Fillinia* sp. This additional natural food could boost fish growth and all related traits. Taken together our results show that the combination of inadvertent hybridization and mass selection have already enhanced the salinity tolerance of Sukamandi strain, making it a unique and valuable genetic resource for Indonesian tilapia breeding to produce superior strain for tilapia culture.

4.2. Potential for further improvement of the Sukamandi tilapia strain

The moderate heritabilities for all production-related traits indicate the presence of sufficient additive genetic variance for future selection on these traits to produce significant responses. Our estimate of h^2 for HW in the brackish water (0.35) is higher compared to what has been estimated for growth in intensive (0.19 ± 0.07) and extensive systems (0.17 ± 0.06) in molobicus hybrid tilapia strain (de Verdal et al., 2014) but is lower compared to what has been reported in previous studies for Nile tilapia grown in saline environments (0.53–0.57; Thoa et al. (2016) and Ninh et al. (2014)). It is possible that the large fluctuation in salinity in this study (6-25 ppt) inhibited the Sukamandi strain from expressing its full genetic potential for growth. Alternatively, the difference in heritability could be due to strain differences. The Sukamandi strain is of hybrid origin and has been selected for 4 generations in brackish water.

We encountered problems with including common environmental effect (c^2) in our models, most likely due to shallow pedigree information and limited pedigree connections between families. Our dataset consisted mostly of full-sibs families and very few half-sib families. Consequently, genetic correlations between observed traits within and between environments were obtained from models without the common environmental effect and this can influence estimates of genetic variance. Maluwa et al. (2006), Trọng et al. (2013) and Omasaki et al. (2016) also reported that a multivariate model to estimate genetic correlation including a common environmental effect did not converge. Not including c^2 usually leads to over-estimated heritability's, as common environmental effects are absorbed in the additive genetic variance component. Expressing growth as DGC makes it less dependent of initial (i.e. pre-tagging) body weight which is the stage most affected by common environmental effects (Bureau et al., 2000; Cho, 1992; Trọng et al., 2013). This trait represents grow out period from stocking to harvest, while harvest weight is a cumulative growth from spawning to harvest. The estimated heritability for DGC in our study agrees with (Trọng et al., 2013) who also omitted c^2 from the model.

Our estimates for all growth parameters showed substantial GxE between brackish and freshwater ponds. The between-environment genetic correlation for DGC was 0.65 (0.09), which suggests substantial re-ranking of genotypes between the two environments. Significant GxE was also reported for HW of Nile tilapia tested in brackish water and freshwater ponds by Luan et al. (2008) at 0.45 ± 0.09. The design of our experiment followed the recommendation of Sae-Lim et al. (2010) with ~1000 fish/environment with equal representation of families, so we assume that our estimates are unbiased. However, the number of fish/environment did not solve the structure problem in our estimation when the number of half-sib families is low, resulted in not converge in the model. GR(L), K, GSI, GW and MS were also indicated substantial GxE between brackish and freshwater. However, small sample size at 6 fish per family for all reproductive traits due to logistical reason resulted in very high standard error, and not estimable GxE of GSI in females as shown in Table 7.

4.3. Implications for future breeding program

To date, the breeding program has been based on selection for own performance (mass selection) for harvest weight, conducted in various shrimp farm environments. The advantage of this breeding scheme is the high accuracy of selection due to selection on own growth performance in brackish water. However, this breeding scheme has several drawbacks related to high mortality of selection candidates during the grow out period in unpredictable salinity condition, security issues, and mortality during the transportation and adaptation from the testing site to the selection site in freshwater. There is also a potential risk in disease transfer from the test pond in brackish water to the brood stock facility in freshwater. Another issue is related to escapees during the grow-out of selection candidates that potentially spread into the natural brackish water environments. To avoid this, closed and restricted testing facilities should be implemented to prevent this threat. Furthermore, reducing the reproductive performance of tilapia in brackish water is desired and could be included in the selection criteria. However, this has positive impact to the environmental and negative consequences to breeding program. The negative consequence could be related to the mating problem to produce sufficient number of families in the next generation.

A shift from brackish water to freshwater pond for fish selection could minimize some of these downsides. However, when G × E interactions are strong, it could result in a reduction in genetic gain due to inaccurate selection of breeding candidates in freshwater (Mulder and Bijma, 2005). *Re*-ranking of genotypes is not substantial if the genetic correlation between environments is above 0.8 (Robertson, 1959). In this study, however, the genetic correlation was 0.65, which means that it is essential to incorporate information from full-sibs in brackish water. Further, combining own performance in freshwater with sib records in brackish water could increase the accuracy of selection and maximise the genetic gain. With own-performance records, we can exploit within-family variation to increase accuracy compared to using only sib information. In practical terms, a sib selection program has several advantages: eliminating transportation costs of testing fish and selection candidate from brackish water to freshwater, and reducing chance of disease transfer from the test pond in BW to the nucleus in FW.

5. Conclusion

Our results show that brackish water ponds provided a positive environment for the Sukamandi strain. However, there was substantial re-ranking shown by genetic correlations of 0.65–0.74 in all observed growth traits. Based on this, we suggest to perform a nucleus breeding program in freshwater and incorporate sib information from brackish water ponds to increase the accuracy of breeding value estimation and to optimize genetic gain.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that has been used is confidential.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aquaculture.2022.738626.

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