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Evaluation of growth performance and genetic analysis of rainbow trout (*Oncorhynchus mykiss*) reared in freshwater and seawater in Japan

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Abstract: Rainbow trout is a globally important aquaculture species and has traditionally been cultured in freshwater. Recently, production of rainbow trout in seawater has been increasing due to its potential for faster growth relative to rearing in freshwater. However, a high mortality during adaptation from freshwater to seawater and growth retardation during subsequent rearing period often occur. This study aimed to evaluate the genetic potential for growth and survival of rainbow trout in seawater rearing and to validate the effectiveness of genomic selection (GS) for these traits. Two populations, designated as A and B, were subjected to both freshwater and seawater growth trials. Using GRAS-Di analysis, 11,105 biallelic SNPs were identified in these fish. Survival rate in the seawater rearing was 43.8% for population A and 49.8% for population B, respectively, with the mortality being observed among the sexually matured individuals. Body weight and standard length showed positive correlations between the values in freshwater and seawater (Pearson's r = 0.55). Narrow-sense heritability for growth traits was estimated using the GBLUP method, which revealed moderate values of heritability in seawater (0.57 for standard length, 0.50 for body weight). Genomic estimated breeding values (GEBV) were calculated and a correlation of 0.25 was obtained between GEBV for body weight in freshwater and seawater. Cross-validation demonstrated predictive accuracies of 0.80 and 0.54 for the body weights in freshwater and seawater, respectively. These results indicate a potential for genetic improvements through GS in the growth and survival of rainbow trout in seawater, providing valuable insights for the sustainable aquaculture practices.

Key words: rainbow trout, selective breeding, growth, SNP, GBLUP

Introduction

Rainbow trout (*Oncorhynchus mykiss*) is a globally significant aquaculture species due to its rapid growth, adaptability, and high market value (FAO 2022). This species, native to North America, has been successfully introduced and cultured worldwide. In Japan, it was first introduced in 1877, and since then has been continuously bred in various aquaculture facilities and research institutions (Hasegawa 2020; Uchino *et al*. 2021). Traditionally, rainbow trout aquaculture has primarily been practiced under freshwater environments. Recently, there is a growing trend towards seawater aquaculture of rainbow trout, as evidenced by the

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successful practices in Nordic countries like Norway (Aas *et al*. 2022). Similarly, seawater aquaculture of this species in Japan has also been developing. Seawater rearing of rainbow trout offers various potential such as growth acceleration and larger-scale production. However, this challenge often brings a high mortality during seawater acclimation as well as growth retardation (Morro *et al*. 2021). Despite these problems and increasing importance of seawater aquaculture for rainbow trout, studies on the genetic potential to improve the growth and survival in seawater are still limited.

As for freshwater aquaculture, selective breeding of this species has been undertaken, focusing on selected key production traits such as growth and disease resistance, and contributed significantly to the sustainability and profitability of rainbow trout aquaculture (Yáñez *et al*. 2014; Yáñez *et al*. 2023). In recent years, the advance in the selection technologies such as genomic selection (GS) has begun to replace the traditional pedigree-based selection, as GS is a powerful tool for accelerating genetic improvement in aquaculture species (Song *et al*. 2023). For rainbow trout, developments of the technologies for constructing high-quality reference genome and obtaining genome-wide single nucleotide polymorphism (SNP) markers, including SNP arrays, genotyping-by-sequencing (GBS) and low-coverage whole-genome sequencing (lcWGS), have enabled the implementation of GS (Palti *et al*. 2015; Bernard *et al*. 2022; Liu *et al*. 2024). The effectiveness of GS in rainbow trout with the use of these genomic resources, has been validated for numerous traits such as high growth rate, disease resistance, thermal tolerance, and hypoxia tolerance (Yoshida and Yáñez 2022; Prchal *et al*. 2023; Yáñez *et al*. 2023). Thus, the applicability of GS to improve the growth and survival of rainbow trout in seawater culture should be evaluated. As a first step, this requires the acquisition of growth and survival data from seawater-cultured rainbow trout, coupled with the validation of trait heritability.

This study aims at evaluating the genetic potential for growth and survival of rainbow trout in seawater using GS. Specifically, we conducted growth trials under both freshwater and seawater rearing conditions using two rainbow trout populations, designated here as A and B. We collected growth data from both freshwater and seawater rearing conditions and subsequently compared them. Furthermore, genome-wide SNP data were obtained using the GRAS-Di method (Hosoya *et al*. 2019). The efficacy of genomic selection for growth in the seawater culture was then assessed by evaluating the genetic parameters and estimating genomic breeding values (GEBV) via the GBLUP approach. This research will provide valuable insights into the genetic architecture of key traits and contribute to the development of improved rainbow trout strains for sustainable and efficient aquaculture in Japan.

Materials and Methods

Experimental fish and growth trials in freshwater and seawater

The production of experimental fish and the freshwater growth trials were conducted at Fuji Trout Hatchery, Shizuoka Fisheries and Marine Technology Institute (Shizuoka, Japan). Population A was established on November 13, 2019, through a full diallel mating of seven parental fish from four strains: Shizuoka Donaldson, Shizuoka steelhead, Shizuoka 4-year-matured, and Shizuoka farmed broodstock. These four strains had been maintained at Fuji Trout Hatchery. Population B was established on December 2, 2020, through a full diallel mating of eleven parental fish from four strains: Shizuoka farmed broodstock, Shizuoka spring spawning, Tochigi farmed broodstock and Tochigi Donaldson. Of these four strains, the former two had been maintained at Fuji Trout Hatchery, and the latter two at Nikko Field Station, Fisheries Technology Institute, Japan Fisheries Research and Education Agency (Tochigi Japan). Fertilized eggs from populations A and B were disinfected with povidone-iodine solution (50 ppm) for 15 min before water hardening to prevent vertical transmission of *Flavobacterium psychrophilum* (Kumagai and Nawata 2010) and then placed in incubation trays at 10 °C until hatching. The hatched fish from both population A and B were reared in 10 °C freshwater at a flow rate of 1.8 kL/h. Fish were fed twice daily with commercial feeds (Twin Power, Nippon Nosan Kogyo, Kanagawa, Japan). The daily amount of feed supplied was determined based on the body weight and water temperature according to the Leitritz feeding chart. At approximately one year post-hatching, fish were injected with PIT tags for individual identification. Standard length and body weight were measured for population A on October 11, 2021 (698 days post-fertilization), and for population B on November 28, 2022 (726 days post-fertilization), to evaluate the growth performances during the freshwater rearing period.

Growth experiments of population A and B in seawater were performed at Miyazu Field Station, Fisheries Technology Institute, Japan Fisheries Research and Education Agency (Kyoto, Japan). Fish used in the seawater growth experiments were 751 days post-fertilization for population A and 737 days post-fertilization for population B. The fish were acclimated

to seawater in a stepwise manner. First, they were held for 24 h in 50% seawater (16‰ salinity), followed by 24 h in 75% seawater (25‰ salinity), and then they were transferred to UV-sterilized seawater (33-34‰ salinity) at a flow rate of 15 kL/h. Seawater rearing was initiated for population A on December 6, 2021, and for population B on December 11, 2022. The fish were fed five times daily with commercial feeds (Kurenai, Nippon Nosan Kogyo, Kanagawa, Japan). To prevent sexual maturation, a long-day photoperiod was provided from 05:00 to 21:00 using LED lights. The seawater rearing temperature for population A ranged from 10°C to 17°C, while that for population B ranged from 11°C to 18°C. The growth experiments ended for population A on May 19, 2022 (165 days after the start of seawater rearing), and for population B on May 17, 2023 (157 days after the start of seawater rearing). Standard length and body weight were measured at the conclusion of each experiment.

Genetic analysis

Tissue samples from the ventral fin were collected from 195 individuals in population A and 273 individuals in population B, and preserved in 99.5% ethanol. Genomic DNA was extracted using InnuPure C96 and smart DNA prep (a) (Analytik Jena, Jena, Germany), following the manufacturer's instructions. A GRAS-Di library was constructed (Hosoya *et al*. 2019), and sequence data were obtained by 150 bp paired-end sequencing using NovaSeq 6000 system (Illumina, San Diego, CA, USA). Library construction and sequencing were performed by Genebay Co., Ltd. (Kanagawa, Japan). Illumina Nextera adapter sequences and low-quality reads were removed using Trimmomatic v.0.39 (Bolger *et al*., 2014) with the following parameters: LEADING, 30; TRAILING, 20; SLIDINGWINDOW, 4:25; ILLUMINACLIP, 2:30:10; MINLEN, 50. The obtained reads were mapped to the rainbow trout reference genome sequence (Omyk_2.0, 2.3 Gb in genome size) using snap-aligner (Zaharia *et al*. 2011; Ali *et al*. 2025) with the following parameters: -so -F s -F b. Variant calling was performed using elPrep 5 version 5.1.3 (Herzeel *et al*. 2021), and Genome Analysis Toolkit (GATK) version 4.4 with Best Practices Workflow (Van der Auwera *et al*. 2014). SNP filtering using vcftools criteria was set as a maximum read depth of 200 and a minimum genotype quality of 20 (Danecek *et al*., 2011). Missing genotypes in the SNP data were imputed using LinkImputeR software version 1.2.4 (Money *et al*. 2017), with a minimum read depth of 6, a call rate of 0.6, and a minor allele frequency of 1%. Heritability and GEBV were estimated using the GBLUP method with the rrBLUP package version 4.6.1 in R (Endelman 2011), using the SNP data and standard length or body weight under the freshwater or seawater rearing conditions. The prediction accuracy of GEBV for each trait was validated using a 5-fold cross-validation with 10 repetitions.

Results and Discussion

Phenotypes

The phenotypic values of growth-related traits in each population are summarized in Table 1. In population A, phenotype measurements were performed of 445 individuals after freshwater rearing for 698 days post fertilization. The average body weight was 0.92 kg, ranging from 0.41 kg to 1.32 kg. The average standard length was 36.8 cm, ranging from 27.5 cm to 41.8 cm. Subsequently, seawater rearing was conducted for 165 days. The number of individuals surviving at the end of seawater rearing was 195, with a survival rate of 43.8% (Fig.1A). Among the 250 individuals that had died during the seawater rearing period, 44 individuals had developed gonads (ovary or testis). All these individuals died in an early stage of seawater rearing (within 1 month). In the seawater rearing of Atlantic salmon (*Salmo salar*), sexually matured individuals, particularly precocious males, often present a high mortality due to maturation having a negative impact on seawater adaptation (Stien *et al*. 2013). Our results also suggest that the progression of sexual maturity reduces their seawater adaptability. At the end of the seawater rearing period, the average body weight was 2.14 kg, ranging from

Table 1 Growth performance of populations A and B in freshwater and seawater rearing trials

Population		Number of fishes	Date	Standard length (cm)			Body weight (kg)		
				ave.	min.	max.	ave.	min.	max.
A	freshwater	445	211011	36.8	27.5	41.8	0.92	0.41	1.32
	seawater	195	220519	46.1	31.5	58.6	2.14	0.40	4.56
B	freshwater	558	221128	32.4	24.5	39.6	0.63	0.20	1.11
	seawater	273	230517	40.3	28.5	52.7	1.45	0.26	3.49

0.40 kg to 4.56 kg. The average standard length was 46.1 cm, ranging from 31.5 cm to 58.6 cm. Among the 195 individuals that survived at the end of seawater rearing, 26 individuals decreased their body weights compared to the initial weights just before the seawater rearing. These individuals were unlikely to have adapted well to seawater, resulting in almost fasting and subsequent weight loss.

In population B, phenotype measurements were performed of 548 individuals after freshwater rearing for 726 days post fertilization. The average body weight was 0.63 kg, ranging from 0.20 kg to 1.11 kg. The average standard length was 32.4 cm, ranging from 24.5 cm to 39.6 cm. Subsequently, seawater rearing was conducted for 157 days. The number of individuals surviving at the end of seawater rearing was 273, with a survival rate of 49.8 % (Fig.1B). Of the 275 dead individuals examined during the experiment, testis was developed in 31 males and ovary was developed in 1 female. Among these matured individuals, one male died on December 17, 2022, at the beginning of seawater rearing, suggesting a lack of seawater adaptability. The other 31 matured individuals died between February 7th, 2023 and May 16th, 2023. The mortality of fish occurred in March and April could be attributable to the spring maturation rather than the winter maturation. At the end of the seawater rearing period, the average body weight was 1.45 kg, ranging from 0.26 kg to 3.49 kg. The average standard length was 40.3 cm, ranging from 28.5 cm to 52.7 cm. Among the 273 individuals that survived at the end of seawater rearing, 45 individuals decreased their body weights compared to the initial weights just before the seawater rearing. Similar to population A, these individuals were unlikely to have adapted well to seawater, resulting in almost fasting and subsequent weight loss.

The body weights of populations A and B were compared at the end of freshwater rearing and at the end of seawater rearing (Fig.2). A positive correlation was noted between the body weights in the freshwater rearing and seawater rearing. The Pearson's correlation coefficient was 0.55. The seawater rearing seemed to result in a larger dispersion of body weight. This suggests that while individuals with larger body weights after the freshwater rearing tended to be still larger even after the seawater rearing, certain factors such as seawater adaptability may have prevented them from growing consistently in the seawater environment.

Genetic analysis

Following the library preparation for GRAS-Di analysis, 150 bp paired-end sequencing was performed using the

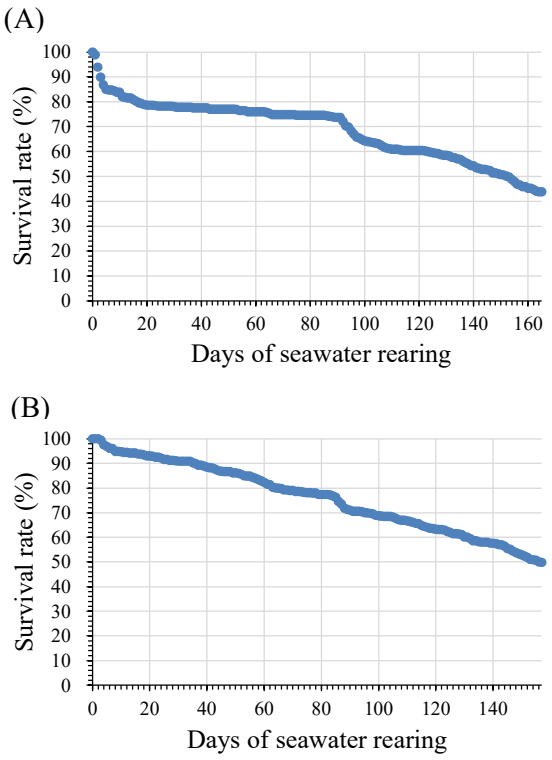

Fig.1 Survival rate after seawater exposure

X-axis represents the number of days after the start of seawater rearing, and Y-axis represents the survival rate (%). (A), population A; (B), population B.

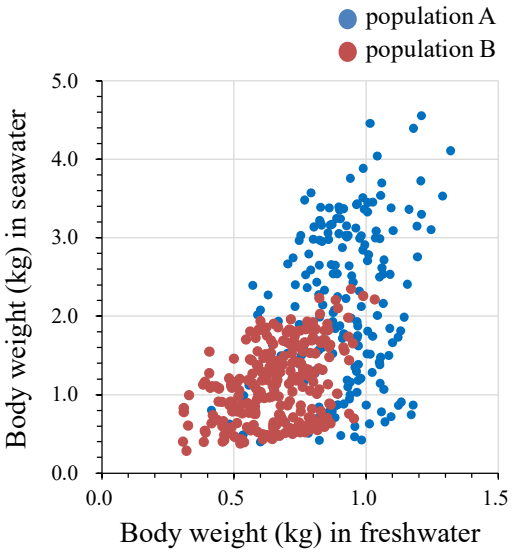

Fig.2 Comparison of body weight in freshwater and seawater

X-axis represents the body weight at the end of freshwater rearing, and Y-axis represents the body weight at the end of seawater rearing. Blue dots indicate the values of population A, and red dots indicate the values of population B.

Table 2 Heritability and prediction accuracy of genomic estimated breeding values for growth-related traits of populations A and B in freshwater and seawater

	heritability		prediction accuracy	
	standard length	body weight	standard length	body weight
freshwater	0.75	0.64	0.76	0.80
seawater	0.57	0.50	0.55	0.54

NovaSeq 6000 system. This sequencing was conducted on the 195 individuals from population A and the 273 individuals from population B, all of which survived at the end of seawater rearing. The sequencing yielded an average of 3.97 million reads and an average of 0.54 Gb per individual. Variant calling yielded 11,105 biallelic SNPs. The narrow-sense heritability for growth traits, specifically body weight and standard body length, was estimated by the GBLUP method using SNP data and is shown in Table 2. The heritability of standard length in the freshwater rearing was 0.75, while that of body weight was 0.64. The heritability of standard length and body weight during the seawater rearing was 0.57 and 0.50, respectively. In the previous report in salmonids, the heritability estimates for body weight measures fell within the range of 0.19-0.50 (Gonzalez-Pena *et al*. 2016). It is important to note that these heritability estimates were obtained in freshwater rearing condition, not in seawater rearing condition (Gonzalez-Pena *et al*., 2016). In the current study, the heritability values of standard body length and body weight in the seawater rearing condition were considered moderate, suggesting a potential for genetic improvement. GEBV for body weight during the freshwater rearing and seawater rearing were estimated using the GBLUP method and then compared (Fig.3). The Pearson's correlation coefficient between GEBV for body weight in freshwater and those in seawater was 0.25. This suggests that the genetic architecture that influence the body weights in the freshwater and seawater environments have some differences. Therefore, selection for body weight in seawater is crucial for the effective selective breeding of rainbow trout that grow rapidly in seawater. The predictive accuracy of GEBV was evaluated by applying cross-validation. In the freshwater rearing period, the predictive accuracy of GEBV for the standard length was 0.76, and that for the body weight was 0.80 (Table 2). In the seawater rearing period, the predictive accuracy of GEBV for the standard length was 0.55, and that for the body weight was 0.54. Gonzalez-Pena *et al*. (2016) reported a prediction accuracy of GEBV as 0.7 for body weight during freshwater

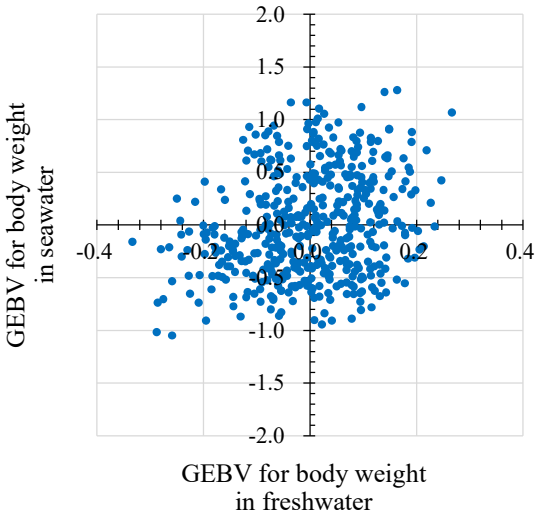

Fig.3 Comparison of genomic estimated breeding values for body weight reared in freshwater and seawater

X-axis represents genomic estimated breeding values (GEBV) for body weight at the end of freshwater rearing, and Y-axis represents GEBV for body weight at the end of seawater rearing.

rearing. In the present study, we obtained a slightly higher prediction accuracy for body weight during the freshwater rearing. The moderate prediction accuracy of GEBV for growth in seawater indicates a benefit potential for the improvement in selection efficiency. Selection of candidate parents for broodstock from individuals rearing in seawater is considered the most effective approach for selective breeding for higher growth in this species. However, returning potential broodstock to freshwater from seawater before use in spawning is often difficult for many rainbow trout farms due to concerns about introducing diseases from external sources. Meanwhile, genomic selection offers a viable alternative approach when availability of future broodstock rearing in seawater is limited. This method suggests that if there are groups of the same origin reared in both seawater and freshwater, potential broodstock can be indirectly selected from the freshwater group based on their GEBV for seawater growth.

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