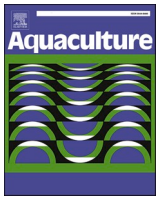
Aquaculture 604 (2025) 742431

Contents lists available at ScienceDirect

Aquaculture

journal homepage: www.elsevier.com/locate/aquaculture



Seasonal variation in two culture systems and genome-wide association analysis of taurine content in the foot muscles of the Pacific abalone (*Haliotis discus hannai*)

Ziheng Yin [a,b,1], Junyu Liu [a,b,1], Wenchao Yu [a,b], Yawei Shen [a,b], Yang Gan [c], Yexin Chen [c], Jinwei Ke [a,b], Xuan Luo [a,b,c], Caihuan Ke [a,b,*], Weiwei You [a,b,*]

[a] State Key Laboratory of Mariculture Breeding, College of Ocean and Earth Sciences, Xiamen University, Xiamen 361102, PR China
[b] Fujian Key Laboratory of Genetics and Breeding of Marine Organisms, Xiamen University, Xiamen 361102, China
[c] Abalone Research Center, Fujian Minruibao Marine Biotechnology Co., Ltd, Xiamen 361102, China

ARTICLE INFO

Keywords:
Pacific abalone
Taurine content
Seasonal variation
GWAS

ABSTRACT

Abalone is one of the most economically valuable shellfish in the world's aquaculture industry, and as production has increased, it has led to a diversification of market quality needs. Taurine, an essential amino acid component, has yet to be well investigated for its seasonal variation and genetically associated genes or loci in Pacific abalone (*Haliotis discus hannai*). In this study, we investigated the variation of taurine content in different seasons under two typical culturing systems in southern China. In addition, we conducted a genome-wide association study (GWAS) with 274 abalone array sequencing and phenotypic data of taurine content. The results revealed that the taurine content showed a trend of significantly decreasing and then increasing with seasonal changes. Individuals farmed in land-based industrial culture system had a greater taurine content than those farmed in sea-based floating raft culture system, with notable differences observed between May and September. A total of 69,530 high-quality SNPs and 274 individuals were identified by quality control. And 32 significantly related SNP loci of taurine content were identified by GWAS, with chromosome 9 hosting the lowest *P* value. A total of 33 candidate genes, including *SLC6A7*, *EGF1*, *B3gnt6*, and *Ptpra*, were annotated. These genes may be connected to amino acid synthesis, transmembrane transport, energy production, protein phosphorylation, and other processes. Among them, genes belonging to the *SLC6A* family may be the key gene taurine content. This study helped us better understand the genetics of the taurine content of Pacific abalone.

1. Introduction

Aquaculture has emerged as one of the world's fastest-growing and most traded food industries, with Asia currently accounting for 90 % of worldwide production (Stentiford et al., 2020). Abalone, a representative marine shellfish, is highly valued as a seafood delicacy in Asian market due to its rich nutritional profile and numerous health benefits (Kim and Pallela, 2012; Shi et al., 2020). China is the world's largest producer of abalone, producing 244,991 tons of cultivated abalone in 2023, making up more than 90 % of the entire production worldwide (Wang and Gao, 2024). The Pacific abalone, *Haliotis discus hannai*, is naturally distributed in parts of the Yellow Sea and Bohai Sea, the Korean Peninsula, and the coasts of Hokkaido (You et al., 2021). Around 2000, abalone farming gradually extended from its natural temperate habitat to subtropical regions. Due to longer periods of suitable temperatures in southern China, the growth period of Pacific abalone has been greatly shortened, making it the main abalone species used for aquaculture.

Recently, there has been a growing demand for high-quality dietary protein from aquatic products (Ghosh et al., 2012). As a delicious marine product, abalone is an excellent source of essential fatty acids, amino acids, and bioactive molecules that meet modern nutritional requirements. It contains high levels of protein and low levels of fat, making it a nutritious and healthy seafood option (Lou et al., 2013; Suleria et al., 2017). The animal body contains large amounts of taurine in many different tissues, including the heart, liver, neurological system,

* Corresponding authors at: State Key Laboratory of Mariculture Breeding, College of Ocean and Earth Sciences, Xiamen University, Xiamen 361102, PR China.
E-mail address: wwyou@xmu.edu.cn (W. You).
[1] These two authors contributed equally to this work.

https://doi.org/10.1016/j.aquaculture.2025.742431
Received 17 October 2024; Received in revised form 8 February 2025; Accepted 12 March 2025
Available online 18 March 2025

and visual system (Franconi et al., 1995). Over the last few decades, research has demonstrated the various biological activities of taurine. Taurine can improve metabolism (Yun et al., 2012; Yun et al., 2011), boost brain growth (Gu et al., 2015), improve eyesight (Huang et al., 2014), reduce tiredness (Geiß et al., 1994), act as an antioxidant (Sirdah, 2015), etc. As a result, taurine has found extensive use in both clinical treatment and dietary additives (Azuma et al., 1992; Militante and Lombardiniab, 2001). Taurine is abundant in abalone foot muscle, with studies on the nutritional quality-related traits of Pacific abalone revealing that the muscle's taurine level can exceed 80 mg/g and the moderate heritability (Liu et al., 2024). As a result, selective breeding for taurine content has the potential to significantly improve quality attributes in the future.

The increased water temperature can cause changes in nutrient metabolism; for example, it can result in an accelerated breakdown of amino acids in fish (Geda et al., 2012). As the temperature rises, the abalone's respiration and metabolism are suppressed, which results in internal energy imbalances and metabolic disorders (Hoegh-Guldberg and Bruno, 2010; Shen et al., 2021). Ectothermic animals accomplish adaptations through metabolic changes and energy turnover. When environmental temperatures change, the relocated energy is used to restore physiological homeostasis (Lermen et al., 2004; Romo et al., 2010; Wu et al., 2021). In the study of juvenile South African abalone (*Haliotis midae*) exposed to higher temperatures and hypoxia, substrate utilization models switched from glycogen/lipid-driven metabolism to protein-driven metabolism (Vosloo et al., 2013). Therefore, it is essential to have a thorough understanding of the taurine content of Pacific abalone in the context of increasing ocean temperatures.

The genome-wide association study (GWAS) is an effective method for locating genes and genetic markers associated with intricate traits (Wellek and Ziegler, 2009). In recent years, the GWAS has been employed increasingly in aquaculture breeding due to the declining cost of sequencing. It has also been used to identify candidate genes for commercially important traits in various aquaculture species, including growth (Ning et al., 2019; Peng et al., 2021), and resistance traits (Jin et al., 2017; San et al., 2021). Furthermore, GWAS research on quality traits in aquatic species has been extensively examined. The GWAS of nutrient traits in 427 Pacific oysters (*Crassostrea gigas*) collected from worldwide found three node SNP regions, which were identified to be connected to the contents of aspartic acid, protein, and glycogen (Meng et al., 2019). According to our previous report, the *slit2*, *fgfr2*, *gria4*, *hnrnpm*, and *megf11* genes were found by GWAS of the glycogen and protein content of Pacific abalone (Liu et al., 2023). These genes may be connected to energy metabolism, transmembrane transport, and immune regulation.

In southern China, sea-based floating raft culture and land-based industrial culture are the main abalone culture systems (Gao et al., 2023). In the present study, the taurine content of Pacific abalone muscle under two commonly cultured systems was examined over four months including February, May, September, and December. The results of seasonal and spatial variations in the composition of Pacific abalone will provide valuable insights for the management of abalone farming to cope with future global climate change and the identification of optimal market times. Furthermore, we analyzed the taurine content of Pacific abalone using GWAS to resolve the genetic structure and identify the relevant SNP loci and genes, which will aid in future genomic selection (GS) for taurine content.

2. Materials and methods

2.1. Sample collection and preparation

A total of 1200 Pacific abalone with the same genetic background and similar sizes were randomly selected, and placed at Jinjiang (JJ), Fujian Province, China (land-based industrial culture) and Dongshan (DS), Fujian Province, China (sea-based culture), where they were cultured with the same density. Furthermore, the same *Gracilaria lemaneiformis* was used as feed for them. Samples were collected at four-time points (February, May, September, and December) based on the annual average temperature of seawater in Fujian Province, where the water temperature reached its maximum value in September (28 °C to 29 °C) and minimum in February (14 °C to 15 °C) (Yu et al., 2021). At each sampling time, 30 abalone were randomly selected from each location, and their shell length (SL), shell width (SW), and wet weight (WW) were measured using vernier calipers with an accuracy of 0.01 mm and an electronic balance with an accuracy of 0.01 g. The foot muscles were then cut into pieces, placed on dry ice, and immediately transported to the laboratory, where they were stored at −80 °C. Each sample was freeze-dried under vacuum for 48 h using a Labconco FreeZone 4.5 L before being crushed to a fine powder for the analysis of taurine. All samples were also randomly mixed and used for the measurement of taurine, which was done three times.

For GWAS analysis, 274 Pacific abalone were chosen at random from a 30-month-old base population in May 2020. The ancestors of this population were the hybrid G2-generation groups from different geographical locations in China (including Jinjiang in Fujian, Yangxia in Fujian, Dalian in Liaoning, Dongshan in Fujian, and Changdao in Shandong). It satisfied the GWAS analysis criteria with a variety of population sources. After measuring the shell length, shell width, and wet weight, the foot muscle was taken and eluted three times with 75 % alcohol until completely dehydrated and stored in 95 % alcohol for subsequent DNA extraction and sequencing. The remaining foot muscles were stored in a refrigerator at −80 °C. Each sample was freeze-dried under vacuum for 48 h using a Labconco FreeZone 4.5 L before being crushed to a fine powder for the analysis of taurine.

2.2. Taurine content analysis

Use an amino acid analyzer to determine the taurine content of the samples. Weigh approximately 0.1 g (accurate to 0.0002 g) of powdered foot muscle into a 15 mL centrifuge tube. Add 4 mL of 4 % sulfosalicylic acid solution and mix well. Following that, use an ultrasonic cell crusher to perform ultrasonic homogenization for 5 min, and the power of the ultrasonic cell crusher was set at 100 watts. To ensure the full extraction of taurine in the sample while preventing its breakdown owing to excessive heat, an ice water bath was also employed for chilling throughout the process, with 20-second intervals per minute. Finally, centrifuge the mixture for 10 min at a speed of 12,000 rpm. Then, the supernatant is transferred to 25 mL volumetric flasks, and the precipitates using the previously described procedure, the precipitate is extracted once again. The combined supernatant was then thoroughly mixed and fixed with a solution of 0.02 mol/L hydrochloric acid. An amino acid analyzer was used to measure the taurine content of the sample after the solution had been filtered through a 0.45 μm membrane and moved to the sample bottle.

2.3. Individual genotyping

In our previous study, the samples were sequenced using the Pacific abalone 40 K multiple single nucleotide-polymorphism (mSNP) array (Liu et al., 2022). Using PLINK software, the sequencing files were filtered to eliminate loci of the following types: (1) loci with a minimum allele frequency of less than 5 %; (2) loci with more than two allele counts; (3) loci with a missing rate of more than 20 % for each individual sample; and (4) loci with a locus missing rate greater than 10 %. It was possible to get a genotype information file with 69,530 SNPs from 262 samples.

2.4. GWAS and candidate gene annotation

To reduce the impact of false-positive loci on the results, the sample population was analyzed using principal component analysis using the

PCA parameter in PLINK before GWAS, identifying population stratification.

Genome-wide association analysis was performed using GEMMA software (Zhou and Stephens, 2012). The result-setting threshold value was corrected using Bonferroni correction, the gray dotted line represents the significance threshold $-\log10(1/N) = 4.84$ (where N is the number of all SNPs). However, this correction was too stringent. The significance threshold was set as $-\log10(1/K) = 3.58$ (where K is the number of SNPs on a single chromosome) (black line) to reduce the false positive rate while maintaining the major significant SNP loci (Peng et al., 2021; Zhou et al., 2019). The CMplot program of R software was utilized to plot Manhattan and Q-Q plots (Yin et al., 2021). Genes with SNP sites located within or closest to upstream and downstream of the SNP sites were identified as potential candidates for taurine content in Pacific abalone.

2.5. Statistical analysis

The means and standard deviations (SD) of each set of data are displayed. Analyses were performed using SPSS Statistics version 27.0 (George and Mallery, 2021). To compare the sample means, ANOVA analyses were conducted, followed by the Tukey HSD test.

3. Results

3.1. The seasonal variation in two culture systems of taurine content

The average seawater temperature in Jinjiang reached a maximum of 27.38 °C in September and a minimum of 14.29 °C in February. Furthermore, in September, the temperature in Dongshan reached 28.17 °C.

In the land-based culture system, the abalone shell lengths were 55.16 mm (February), 65.40 mm (May), 68.58 mm (September), and 72.04 mm (December) in the four seasons, with an average growth rate of 30.6 %; in the sea-based floating raft culture, shell lengths were 55.16 mm (February), 65.40 mm (May), 70.32 mm (September), and 77.32 mm (December), with an average growth rate of 40.2 %. 65.40 mm in May, 70.32 mm in September, 77.32 mm in December, and 55.16 mm in February, with a growth rate of 40.2 % on average (Table. 1).

The taurine content under the two culture systems trended downward and then upward considerably over time (Fig. 1). The one-way ANOVA test findings for the land-based culture system revealed that there was no significant difference in taurine content between February and May or September and December. Except for February and May, when there were no discernible variations in taurine content, there were notable variations in every group for the sea-based floating raft culture system.

3.2. The GWAS individual taurine content

The taurine content of the foot muscles of 262 Pacific abalone was calculated after the missing and abnormal samples were removed. We then plotted the frequency distribution histograms of the samples and found that they followed a normal distribution (Fig. 2). Table 2 displayed the descriptive statistics of the taurine content and the growth-

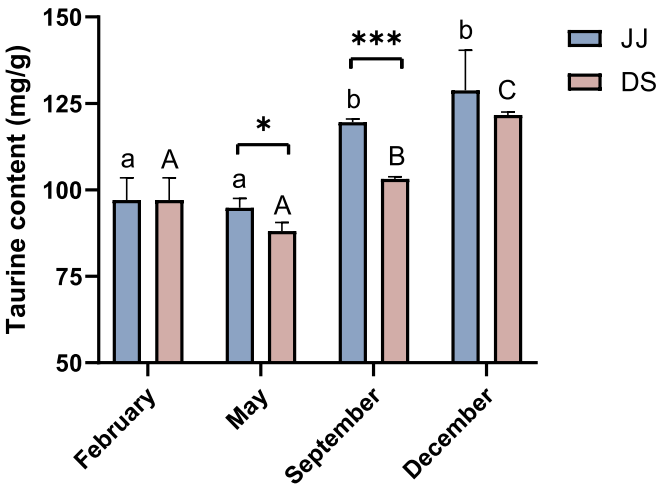


Fig. 1. The taurine content of two culture systems during different seasons. The lowercase letters represent significant differences in taurine content between seasons in the land-based industrial culture system; The uppercase letters represent significant differences in taurine content between seasons in the sea-based culture system; "*" represents significant differences between the two culture systems in the same season.

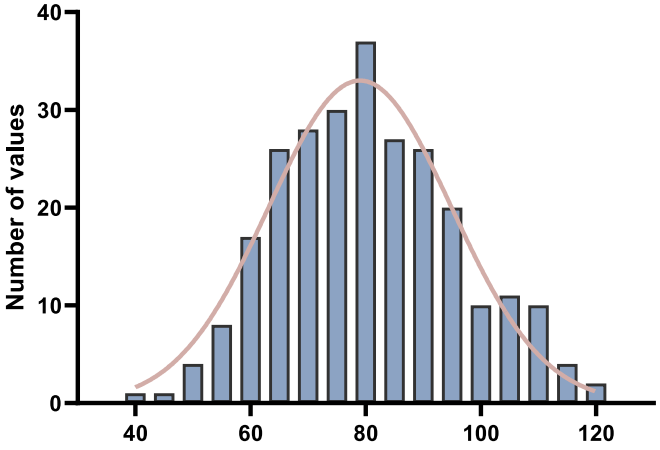


Fig. 2. Distribution statistics of Taurine content of Pacific abalone.

Table 2
Descriptive statistics of phenotypic growth and taurine content traits for GWAS.

Traits	Max	Min	Mean	SD	CV
SL (mm)	93.93	42.40	74.95	8.16	10.89
SW (mm)	91.41	38.57	52.19	5.82	11.16
WW (g)	111.51	25.30	60.66	17.61	29.03
TC (mg/g)	119.77	40.89	80.71	15.44	19.13

SL: shell length; SW: shell width; WW: wet weight; TC: taurine content; CV: Coefficient of variation.

Table 1
Distribution statistics of growth traits of Pacific abalone in different seasons in two culture systems.

Traits	JJ				DS			
	Feb	May	Sep	Dec	Feb	May	Sep	Dec
SL (mm)	55.16 ± 4.13	65.40 ± 5.45	68.58 ± 3.07	72.04 ± 7.82	55.16 ± 4.13	65.40 ± 6.89	70.32 ± 5.89	77.32 ± 5.27
SW (mm)	37.44 ± 2.67	43.48 ± 3.23	45.80 ± 2.42	48.20 ± 4.30	37.44 ± 2.67	43.80 ± 4.63	47.40 ± 4.29	52.35 ± 3.29
WW (g)	23.54 ± 6.20	37.93 ± 9.23	38.49 ± 7.73	47.55 ± 16.98	23.54 ± 6.20	36.97 ± 11.48	45.64 ± 10.66	59.57 ± 13.51

JJ: Jinjiang, Fujian Province, China (land-based industrial culture); DS: Dongshan, Fujian Province, China (sea-based culture); SL: shell length; SW: shell width; WW: wet weight.

related traits. The content ranged from 40.89 mg/g to 119.77 mg/g, with a mean value of 80.71 mg/g and a coefficient of variation of 19.13 %.

3.3. GWAS and putative genes identification

The results of the PCA analysis revealed considerable group stratification of this population (Fig. 3). Then these three PCs were determined as variables to be incorporated into the model for subsequent GWAS to lessen the effects of group stratification.

A total of 32 SNP loci were found to be substantially correlated with the taurine content in the foot muscles of Pacific abalone. The LC18319343 on chromosome 9 was the most significant SNP locus, with a significance *P*-value of 9.95×10^{-6} (Table 3). Furthermore, chromosomes 4 and 9 displayed a clustered distribution of significant SNP loci, and exhibiting the largest number of loci. Fig. 4 displays Manhattan and Q-Q plots of GWAS.

A total of 33 candidate genes, including *SLC6A7*, *EGF1*, *B3gnt6*, and *Ptpra*, were annotated. These genes may be connected to amino acid synthesis, transmembrane transport, energy production, protein phosphorylation, and other processes. The pertinent candidate genes are displayed in Table 4.

4. Discussion

One of the most prevalent free amino acids in tissues, taurine is regarded as a functional amino acid that is crucial for many physiological processes in aquatic animals, including growth, immunomodulation, antioxidant defense, and stress reduction (Güroy et al., 2024). Taurine can be acquired by endogenous synthesis or external intake in aquatic animals, with the liver serving as the primary source of taurine synthesis (Sales, 2009). However, the ability to synthesize taurine varies from species, and even the amount of taurine varies between tissues (Wang et al., 2016). Furthermore, variations in water temperature that are above the appropriate range may impact aquatic animal's physiological and metabolic processes (Kim et al., 2020). Decrease in several amino acids (glutamine, tyrosine, and phenylalanine) and changes in lipid metabolism induced by high temperature in Atlantic salmon (*Salmo salar*) (Kullgren et al., 2013). In this study, there was a little decrease in taurine content from February to May, which could have been caused by the rising temperatures. However, there was a gradual increase in the following months of September and December, which could be related to high temperatures leading to a high consumption of energy substances. The previous reports have shown that the activity and gene expression of enzymes including phosphofructokinase, glucokinase, and glucose transporter protein 2, taurine enhances glucose metabolism (Sampath et al., 2020). When exposed to summertime water temperatures exceeding 28 °C, Pacific abalone, which is endemic to temperate cold-water species, additionally utilizes glycogen as a heat-resistant substance (Jentjens et al., 2002). The synthesis of glycogen under stress may be assisted by an increase in taurine concentration. This finding confirmed the high negative genetic correlation between taurine and glycogen contents (Liu et al., 2024).

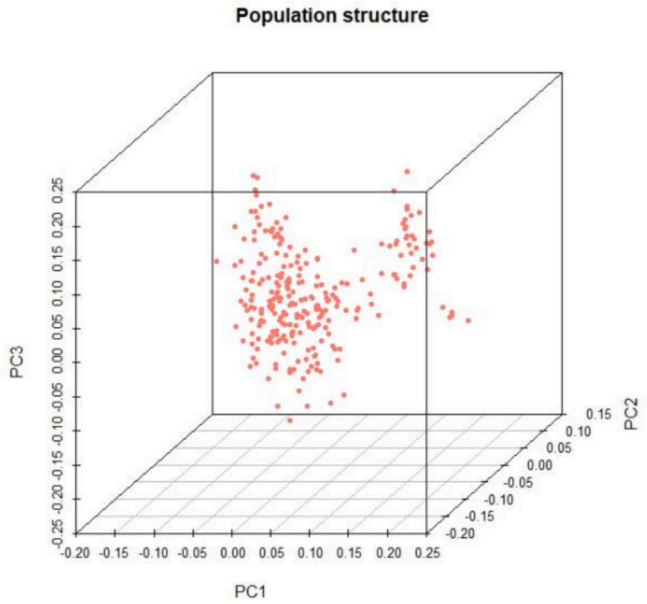


Fig. 3. Principal component analysis (PCA) of the analysis population.

Table 3
SNPs associated with taurine content traits in Pacific abalone.

Chr	Position	SNP	Allele	MAF	*P* value
9	18319343	LC18319343	T/C	0.067	9.95E−06
15	21093168	LC21093168	A/T	0.088	1.35E−05
4	50137351	LC50137351	T/A	0.086	1.49E−05
15	21093167	LC21093167	T/G	0.09	1.69E−05
10	25585499	LC25585499	T/C	0.257	1.97E−05
10	25585500	LC25585500	G/A	0.257	1.97E−05
6	35623333	LC35623333	G/T	0.067	2.87E−05
9	18478003	LC18478003	T/A	0.193	2.91E−05
1	19877259	LC19877259	C/T	0.169	3.58E−05
9	48406953	LC48406953	A/C	0.12	4.57E−05
16	62171683	LC62171683	C/T	0.294	5.27E−05
9	17202789	LC17202789	T/G	0.437	5.27E−05
4	8406545	LC8406545	A/G	0.214	5.30E−05
6	42569597	LC42569597	C/G	0.076	5.47E−05
1	21672433	LC21672433	C/T	0.399	6.38E−05
4	8406458	LC8406458	A/G	0.258	6.77E−05
14	86226025	LC86226025	A/G	0.109	7.06E−05
18	67890438	LC67890438	C/G	0.451	7.31E−05
7	40350143	LC40350143	T/A	0.079	7.50E−05
4	8406494	LC8406494	G/T	0.298	8.79E−05
18	38005134	LC38005134	A/G	0.212	1.28E−04
10	17493111	LC17493111	A/G	0.247	1.33E−04
16	64101470	LC64101470	A/T	0.109	1.67E−04
17	895380	LC895380	C/T	0.429	1.79E−04
14	12983693	LC12983693	T/A	0.385	1.91E−04
4	53568837	LC53568837	C/T	0.416	1.92E−04
5	32536044	LC32536044	G/T	0.353	2.04E−04
6	60515296	LC60515296	C/T	0.063	2.09E−04
1	20185694	LC20185694	A/G	0.275	2.21E−04
7	40350126	LC40350126	A/G	0.098	2.30E−04
9	17471436	LC17471436	C/A	0.122	2.32E−04
1	33235477	LC33235477	A/G	0.141	2.46E−04

Chr: chromosome; Allele: minor/major allele; MAF: Minimum allele frequency.

Quality traits have recently been studied in aquatic animals as a result of selective breeding and commercial demand (Tan et al., 2020). However, it is important to investigate the basic processes and genetic characteristics of quality traits. The GWAS is a useful instrument for linking genetic variation to complex quantitative trait phenotypes and identifying feasible candidate markers and genes for molecular-assisted breeding (Ali et al., 2019). Our GWAS research revealed 32 SNP loci linked with abalone taurine content. These loci were found on multiple chromosomes, however, there was no clear clustered distribution except for chromosomes 4 and 9, which might imply that the characteristic traits are controlled by multiple genes. Similar findings were observed in the amino acid GWAS analysis of Pacific oysters (Meng et al., 2019). Gene annotation results identified 33 genes, such as *SLC6A7*, *EGF1*, *B3gnt6*, *Ptpra*, which play important roles in amino acid synthesis, transmembrane transport, energy synthesis, protein phosphorylation and other biological processes.

Indeed, genes change from season to season, such as in oyster research, it was discovered that variations in glycogen content across the seasons were linked to variations in both *ChGS* and *ChGP* expression (Qin et al., 2021). Additionally, we found some research that suggests that different animals may display distinct behaviors due to varying

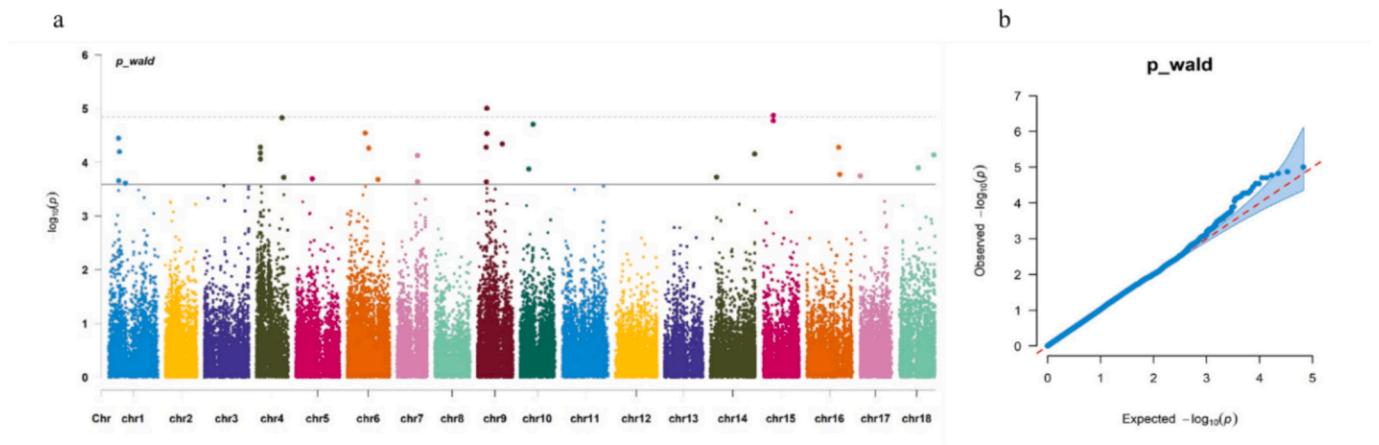


Fig. 4. Manhattan and QQ plot of taurine content in GWAS.

levels of expression of particular genes at varying temperatures. According to a study on Antarctic krill (*Euphausia superba*), all areas exhibit up-regulated summertime expression of essential genes in comparison to wintertime, which helps the animals adjust to their changing environment (Höring et al., 2021). Since different genes change with the seasons, locating the significant genes at a particular time of listing is crucial for genetic selection. During the market season, various phenotypes related to economic traits of aquatic animals are most fully and distinctly exhibited. At this point, GWAS research can more accurately identify the gene loci linked to the economic traits. In the investigations of Asian seabass (*Lates calcarifer*) (Sukhavachana et al., 2022) and Pacific White Shrimp (*Litopenaeus vannamei*) (Lyu et al., 2021), GWAS analyses were performed using individual traits at the time of listing. Thus, we selected the listing season (May) for GWAS.

There are currently 458 transporter proteins within the *SLC* superfamily that carry a variety of chemicals across cell membranes. The *SLC6A* family of transporter proteins uses sodium gradients for the secondary active transport of tiny amino acids or substrates that resemble amino acids, and the *SLC6A6* transporter protein uses taurine as a transport substrate (Bröer and Gether, 2012). Additionally, the *SLC6A6* gene was found in taurine GWAS analysis of Japanese black beef, indicating that selecting for higher taurine concentrations in black beef could be aided by the significant SNP on the telomere side of *SLC6A6* (Sasago et al., 2018). Furthermore, mice with the taurine transporter protein (TauT; *SLC6A6*) knocked out develop taurine-deficient cardiomyopathy, which thins the ventricular wall and induces heart failure (Ito et al., 2018). This implies that a major gene involved in taurine synthesis in animal individuals is probably a member of the *SLC6A* family. Moreover, *Bsgn6* and *Bsgn7* may have an anti-inflammatory effect (Wang et al., 2024; Xiao et al., 2022), and other genes, including *CSMD2* and *CTGF*, have the effect of promoting cell proliferation and differentiation (Gutierrez et al., 2019; Yan et al., 2022). These findings imply that taurine may carry out a variety of functions in organisms. As a result, several of the loci identified by our GWAS may be suitable genes for future confirmation of variations in expression between seasons, and determine if the characteristic of taurine content is changed by gene and environmental interactions.

The accuracy of GWAS analysis results was significantly impacted by high-throughput genotyping data. When compared to technologies like SNP microarray and simplified genome (RAD-Seq), whole genome resequencing offers a clear advantage in terms of the number of loci (Talouarn et al., 2020). We selected the previously independently developed 40 K multiple-SNP array for genotyping in our work, primarily because of the advantages of customized flexibility, high flux, low target sequencing cost, and accurate sequencing results (Liu et al., 2022). Furthermore, the quantity of sequencing samples was another important issue that restricts the accuracy of GWAS results (Fu et al., 2020). Our study employed 274 samples, which is a modest sample size but still reasonably informative. The taurine concentration of other species has also been closely correlated with the genes we found, such as the *SLC6A* family. In the meantime, our results can be analyzed together with multi-omics data in the future to fully resolve the biological functions and regulatory mechanisms of the genes at various levels. This will help to identify the causal genes of the GWAS loci, enhance our understanding of the genetic basis of the taurine content, and increase prediction accuracy in the GS model.

Taurine has been shown in several studies to serve a variety of purposes for aquatic life. The research on yellow catfish (*Pelteobagrus fulvidraco*) that taurine plays an important role when fish experience oxidative stress (Zhang et al., 2018). By including taurine in their diet, the ability to function as an antioxidant was increased through the upregulation of genes linked to antioxidant enzymes. In grass carp (*Ctenopharyngodon idella*) a comparable outcome was also verified (Sun et al., 2024). Extensive research has demonstrated that taurine may improve the immune system; in experiments with *Litopenaeus vannamei*, taurine was discovered to be able to both dramatically improve the immune system and prevent the development of apoptosis (Shi et al., 2023). Furthermore, the organism suffers a variety of modifications in response to high temperatures, and taurine assists in reducing this stress reaction, as evidenced by research on carp and tilapia, in which taurine seems to offset modest temperature-induced alterations in muscle histidine and N-α-acetyl histidine (Geda et al., 2017). Additionally, taurine was found to enhance heart thermotolerance by raising Hsp70 supersomes, as demonstrated by a rainbow trout study (Luo, 2020). Moreover, the study on broilers had confirmed, broilers elevate plasma taurine levels for self-protection, implying that individuals with higher levels of taurine may be more resistant to stress (Ruiz-Feria et al., 1999). This is also lined up with our research, which showed that over the time of rising water temperatures from May to September, the taurine content in the foot muscles of Pacific abalone gradually increased in response to high-temperature stress. Currently, breeding objectives are shifting from purely production-oriented goals to more balanced approaches that enhance both performance and robustness. Robustness, de-fined as the ability to resist or recover from disturbances, which correlates with improved health and survival in various species. Especially in aquaculture, it is increasingly important due to pathogen mutations and environmental complexity, some traits such as swimming performance in large yellow croaker (Larimichthys crocea) (Zeng et al., 2023) and carotenoid content in scallops (*Chlamys nobilis*) (Zhang et al., 2021) have been linked to robustness. In conclusion, the benefit of indirect selection in Pacific abalone is the fact that it selects for genes or combinations of genes linked with high taurine concentration. These genes may regulate taurine production and accumulation, resulting in greater taurine levels in response to stress, indicating improved robustness. Meanwhile,

Table 4
Genes associated with taurine content traits of Pacific abalone.

Chr	Location (bp)	Gene name	Gene annotation
1	20,196,168–20,199,231	*DCST2*	DC-STAMP domain-containing protein 2
1	21,668,480–21,681,411	*ZNF235*	Zinc finger protein 235 OS=*Homo sapiens*
1	33,227,653–33,242,197	*SCNN1B*	Amiloride-sensitive sodium channel subunit beta
1	19,959,491–19,973,083	*LPAR6*	Lysophosphatidic acid receptor 6
1	19,778,013–19,779,571	*B0563.6*	Probable G-protein coupled receptor B0563.6
4	50,134,849–50,138,871	*MIMI_L93*	Putative ankyrin repeat protein L93
4	8,250,248–8,251,560	*SPBC660.12c*	Uncharacterized aminotransferase C660.12c
4	8,497,222–8,596,066	*CTGF*	Connective tissue growth factor
5	32,523,519–32,552,396	*YajO*	Uncharacterized oxidoreductase YajO
6	60,482,688–60,486,565	*vlpE*	Variant surface antigen E
6	35,447,228–35,453,918	*CSMD2*	CUB and sushi domain-containing protein 2
6	42,553,904–42,593,500	*ABCC1*	Multidrug resistance-associated protein 1
6	60,572,795–60,636,250	*EGF1*	Fibropellin-1
7	40,373,490–40,394,695	*FGFR2*	Fibroblast growth factor receptor 2
9	18,502,953–18,516,542	*dbx1a*	Homeobox protein DBX1-A
9	17,875,208–17,876,215	*B3gnt6*	UDP-GlcNAc:betaGal beta-1,3-*N*-acetylglucosaminyltransferase 6
9	17,123,558–17,124,468	*B3gnt7*	UDP-GlcNAc:betaGal beta-1,3-*N*-acetylglucosaminyltransferase 7
9	18,354,689–18,359,537	*Dl*	Neurogenic locus protein delta
9	48,371,092–48,400,841	*Ank2*	Ankyrin-2
9	48,410,274–48,437,414	*CG7872*	DnaJ homolog subfamily C member 25 homolog
10	17,475,373–17,475,708	*Ehmt1*	Histone-lysine *N*-methyltransferase EHMT1
10	25,585,006–25,590,664	*NSNH*	Inosine-uridine preferring nucleoside hydrolase
14	12,944,047–12,953,826	*TRIM3*	Tripartite motif-containing protein 3
14	13,000,396–13,001,176	*Trim2*	Tripartite motif-containing protein 2
14	86,182,350–86,224,805	*Ptpra*	Receptor-type tyrosine-protein phosphatase alpha
15	21,019,935–21,125,758	*AKAP17A*	A-kinase anchor protein 17A
16	62,158,152–62,158,946	*SF3A2*	Splicing factor 3A subunit 2
16	63,911,906–64,061,044	*FLII*	Protein flightless-1 homolog
16	62,211,559–62,233,473	*ENGASE*	Cytosolic *endo*-beta-*N*-acetylglucosaminidase
18	67,862,259–67,884,504	*SRPX2*	Sushi repeat-containing protein
18	38,009,498–38,040,473	*RGSL1*	Regulator of G-protein signaling protein-like
18	67,941,042–67,951,431	*SLC6A7*	Sodium-dependent proline transporter
18	37,967,937–37,991,115	*Kars*	Lysine–tRNA ligase

taurine may also affect the flavor and quality of flesh from animals. The muscle quality of European sea bass (*Dicentrarchus labrax*) was found to be considerably impacted by the addition of taurine to the diet, resulting in reduced fillet elasticity (Kotzamanis et al., 2020). The taurine level of the meat was shown to be strongly linked with the panel's assessment of the freshness of the products it evaluated in a study with Japanese black cattle (Suzuki et al., 2017). As such, based on the rich biological functions of taurine and its effect on meat quality, increasing taurine content in abalone may be a future breeding objective, which may lead to an increase in muscle quality while enhancing its robustness.

5. Conclusion

We investigated seasonal variations in taurine in Pacific abalone foot muscles under two culture systems, and performed GWAS analyses on 274 Pacific abalone individuals, which detected a total of 32 SNP loci significantly associated with taurine content. The taurine content of abalone was shown to be substantially correlated with 33 genes, including the essential gene *SLC6A7* for further validation. Our findings contribute to the knowledge about the yearly variation in taurine content in abalone foot muscles. Furthermore, the identified genes may be further confirmed as taurine markers, which would facilitate the improvement of Pacific abalone quality in further studies.

CRediT authorship contribution statement

Ziheng Yin: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation. **Junyu Liu:** Writing – review & editing, Writing – original draft, Software, Methodology, Data curation. **Wenchao Yu:** Software, Formal analysis. **Yawei Shen:** Methodology, Investigation. **Yang Gan:** Methodology, Investigation. **Yexin Chen:** Methodology, Investigation. **Jinwei Ke:** Supervision, Resources. **Xuan Luo:** Validation, Supervision, Resources, Investigation. **Caihuan Ke:** Supervision, Resources, Funding acquisition, Conceptualization. **Weiwei You:** Writing – review & editing, Validation, Project administration, Investigation.

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.

Acknowledgments

This work was supported by grants from National Natural Science Foundation of China (No. U22A20530), Seed Industry Innovation and Industrialization in Fujian Province (No. 2021FJSCZY02), Earmarked Fund for CARS (No. CARS-49). We'd like to express our gratitude for the assistance provided by the Germplasm Resource-sharing Platform of Aquatic Species in Fujian Province.

Data availability

Data will be made available on request.

References

Ali, A., Al-Tobasei, R., Lourenco, D., Leeds, T., Kenney, B., Salem, M., 2019. Genome-wide association study identifies genomic loci affecting filet firmness and protein content in rainbow trout. Front. Genet. 10, 386. https://doi.org/10.3389/fgene.2019.00386.

Azuma, J., Sawamura, A., Awata, N., 1992. Usefulness of taurine in chronic congestive heart failure and its prospective application. Jpn. Circ. J. 56 (1), 95–99. https://doi.org/10.1253/jcj.56.95.

Bröer, S., Gether, U., 2012. The solute carrier 6 family of transporters. Br. J. Pharmacol. 167 (2), 256–278. https://doi.org/10.1111/j.1476-5381.2012.01975.x.

Franconi, F., Bennardini, F., Mattana, A., Miceli, M., Ciuti, M., Mian, M., Gironi, A., Anichini, R., Seghieri, G., 1995. Plasma and platelet taurine are reduced in subjects with insulin-dependent diabetes mellitus: effects of taurine supplementation. Am. J. Clin. Nutr. 61 (5), 1115–1119. https://doi.org/10.1093/ajcn/61.5.1115.

Fu, L., Jiang, Y., Wang, C., Mei, M., Zhou, Z., Jiang, Y., Song, H., Ding, X., 2020. A genome-wide association study on feed efficiency related traits in landrace pigs. Front. Genet. 11, 692. https://doi.org/10.3389/fgene.2020.00692.

Gao, X., Zhang, M., Luo, X., You, W., Ke, C., 2023. Transitions, challenges and trends in China's abalone culture industry. Rev. Aquac. 15 (4), 1274–1293. https://doi.org/10.1111/raq.12769.

Geda, F., Rekecki, A., Decostere, A., Bossier, P., Wuyts, B., Kalmar, I.D., Janssens, G.P.J., 2012. Changes in intestinal morphology and amino acid catabolism in common carp at mildly elevated temperature as affected by dietary mannanoligosaccharides. Anim. Feed Sci. Technol. 178 (1), 95–102. https://doi.org/10.1016/j.anifeedsci.2012.09.008.

Geda, F., Declercq, A.M., Remø, S.C., Waagbø, R., Lourenço, M., Janssens, G.P.J., 2017. The metabolic response in fish to mildly elevated water temperature relates to species-dependent muscular concentrations of imidazole compounds and free amino acids. J. Therm. Biol. 65, 57–63. https://doi.org/10.1016/j.jtherbio.2017.02.004.

Geiß, K.R., Jester, I., Falke, W., Hamm, M., Waag, K.L., 1994. The effect of a taurine-containing drink on performance in 10 endurance-athletes. Amino Acids 7 (1), 45–56. https://doi.org/10.1007/bf00808445.

George, D., Mallery, P., 2021. IBM SPSS Statistics 27 Step by Step: A Simple Guide and Reference. Routledge.

Ghosh, S., Suri, D., Uauy, R., 2012. Assessment of protein adequacy in developing countries: quality matters. Br. J. Nutr. 108 (Suppl. 2), S77–S87. https://doi.org/10.1017/s0007114512002577.

Gu, Y., Zhao, Y., Qian, K., Sun, M., 2015. Taurine attenuates hippocampal and corpus callosum damage, and enhances neurological recovery after closed head injury in rats. Neuroscience 291, 331–340. https://doi.org/10.1016/j.neuroscience.2014.09.073.

Güroy, D., Karadal, O., Güroy, B., Emre, Y., Emre, N., Eraslan, D., Yalım, F.B., Mantoğlu, S., Demir, A., 2024. Dietary taurine improves the growth performance, health status and liver histopathology of meagre (*Argyrosomus regius*) fed a reduced fish meal diet. Ann. Anim. Sci. 24 (3), 851–866. https://doi.org/10.2478/aoas-2024-0011.

Gutierrez, M.A., Dwyer, B.E., Franco, S.J., 2019. Csmd2 is a synaptic transmembrane protein that interacts with PSD-95 and is required for neuronal maturation. Eneuro 6 (2). https://doi.org/10.1523/eneuro.0434-18.2019. ENEURO.0434-0418.2019.

Hoegh-Guldberg, O., Bruno, J.F., 2010. The impact of climate change on the world's marine ecosystems. Science 328 (5985), 1523–1528. https://doi.org/10.1126/science.1189930.

Höring, F., Biscontin, A., Harms, L., Sales, G., Reiss, C.S., De Pittà, C., Meyer, B., 2021. Seasonal gene expression profiling of Antarctic krill in three different latitudinal regions. Mar. Genomics 56, 100806. https://doi.org/10.1016/j.margen.2020.100806.

Huang, M., Song, J., Lu, B., Huang, H., Chen, Y., Yin, W., Zhu, W., Su, X., Wu, C., Hu, H., 2014. Synthesis of taurine–fluorescein conjugate and evaluation of its retina-targeted efficiency in *vitro*. Acta Pharm. Sin. B 4 (6), 447–453. https://doi.org/10.1016/j.apsb.2014.10.006.

Ito, T., Murakami, S., Schaffer, S., 2018. Pathway analysis of a transcriptome and metabolite profile to elucidate a compensatory mechanism for taurine deficiency in the heart of taurine transporter knockout mice. J 1 (1), 57–70.

Jentjens, R.L., Wagenmakers, A.J., Jeukendrup, A.E., 2002. Heat stress increases muscle glycogen use but reduces the oxidation of ingested carbohydrates during exercise. J. Appl. Physiol. (1985) 92 (4), 1562–1572. https://doi.org/10.1152/japplphysiol.00482.2001.

Jin, Y., Zhou, T., Geng, X., Liu, S., Chen, A., Yao, J., Jiang, C., Tan, S., Su, B., Liu, Z., 2017. A genome-wide association study of heat stress-associated SNPs in catfish. Anim. Genet. 48 (2), 233–236. https://doi.org/10.1111/age.12482.

Kim, S.K., Pallela, R., 2012. Medicinal foods from marine animals: current status and prospects. Adv. Food Nutr. Res. 65, 1–9. https://doi.org/10.1016/b978-0-12-416003-3.00001-9.

Kim, S., Kim, A., Ma, S., Lee, W., Lee, S., Yoon, D., Kim, D.-H., Kim, S., 2020. Glutathione injection alleviates the fluctuation of metabolic response under thermal stress in olive flounder, *Paralichthys olivaceus*. Metabolites 10 (1), 3.

Kotzamanis, Y., Kumar, V., Tsironi, T., Grigorakis, K., Ilia, V., Vatsos, I., Brezas, A., van Eys, J., Gisbert, E., 2020. Taurine supplementation in high-soy diets affects fillet quality of European sea bass (*Dicentrarchus labrax*). Aquaculture 520, 734655. https://doi.org/10.1016/j.aquaculture.2019.734655.

Kullgren, A., Jutfelt, F., Fontanillas, R., Sundell, K., Samuelsson, L., Wiklander, K., Kling, P., Koppe, W., Larsson, D.G.J., Björnsson, B.T., Jönsson, E., 2013. The impact of temperature on the metabolome and endocrine metabolic signals in Atlantic salmon (*Salmo salar*). Comp. Biochem. Physiol. A Mol. Integr. Physiol. 164 (1), 44–53. https://doi.org/10.1016/j.cbpa.2012.10.005.

Lermen, C.L., Lappe, R., Crestani, M., Vieira, V.P., Gioda, C.R., Schetinger, M.R.C., Baldisserotto, B., Moraes, G., Morsch, V.M., 2004. Effect of different temperature regimes on metabolic and blood parameters of silver catfish *Rhamdia quelen*. Aquaculture 239 (1), 497–507. https://doi.org/10.1016/j.aquaculture.2004.06.021.

Liu, J., Peng, W., Yu, F., Lin, W., Shen, Y., Yu, W., Gong, S., Huang, H., You, W., Luo, X., Ke, C., 2022. Development and validation of a 40-K multiple-SNP array for Pacific abalone (*Haliotis discus hannai*). Aquaculture 558, 738393. https://doi.org/10.1016/j.aquaculture.2022.738393.

Liu, J., Zhou, M., Yin, Z., Huang, D., Zhu, L., Zou, W., Yu, W., Shen, Y., Huang, Z., You, W., Ke, C., Luo, X., 2023. Development of near-infrared reflectance spectroscopy (NIRS) model and genome-wide association study for glycogen and protein content in Pacific abalone. Aquaculture 576, 739764. https://doi.org/10.1016/j.aquaculture.2023.739764.

Liu, J., Yin, Z., Zhou, M., Yu, W., You, W., Chen, Y., Luo, X., Ke, C., 2024. Genetic parameters and genomic prediction for nutritional quality-related traits of Pacific abalone (*Haliotis discus hannai*). Aquaculture 579, 740118. https://doi.org/10.1016/j.aquaculture.2023.740118.

Lou, Q.-M., Wang, Y.-M., Xue, C.-H., 2013. Lipid and fatty acid composition of two species of abalone, *Haliotis discus hannai Ino* and *Haliotis diversicolor Reeve*. J. Food Biochem. 37 (3), 296–301. https://doi.org/10.1111/j.1745-4514.2011.00631.x.

Luo, Z., 2020. Effects of Taurine on Growth Performance and Heat Stressed Response of Rainbowtrout (*Oncorhynchus mykiss*). Gansu Agricultural University, Lanzhou, China.

Lyu, D., Yu, Y., Wang, Q., Luo, Z., Zhang, Q., Zhang, X., Xiang, J., Li, F., 2021. Identification of growth-associated genes by genome-wide association study and their potential application in the breeding of Pacific white shrimp (*Litopenaeus vannamei*). Front. Genet. 12. https://doi.org/10.3389/fgene.2021.611570.

Meng, J., Song, K., Li, C., Liu, S., Shi, R., Li, B., Wang, T., Li, A., Que, H., Li, L., Zhang, G., 2019. Genome-wide association analysis of nutrient traits in the oyster *Crassostrea gigas*: genetic effect and interaction network. BMC Genomics 20 (1), 625. https://doi.org/10.1186/s12864-019-5971-z.

Militante, J.D., Lombardiniab, J.B., 2001. Increased cardiac levels of taurine in cardiomyopathy: the paradoxical benefits of oral taurine treatment. Nutr. Res. 21 (1), 93–102. https://doi.org/10.1016/S0271-5317(00)00251-7.

Ning, X., Li, X., Wang, J., Zhang, X., Kong, L., Meng, D., Wang, H., Li, Y., Zhang, L., Wang, S., Hu, X., Bao, Z., 2019. Genome-wide association study reveals E2F3 as the candidate gene for scallop growth. Aquaculture 511, 734216. https://doi.org/10.1016/j.aquaculture.2019.734216.

Peng, W., Yu, F., Wu, Y., Zhang, Y., Lu, C., Wang, Y., Huang, Z., Lu, Y., Chen, N., Luo, X., You, W., Ke, C., 2021. Identification of growth-related SNPs and genes in the genome of the Pacific abalone (*Haliotis discus hannai*) using GWAS. Aquaculture 541, 736820. https://doi.org/10.1016/j.aquaculture.2021.736820.

Qin, Y., Li, X., Li, J., Zhou, Y., Xiang, Z., Ma, H., Noor, Z., Mo, R., Zhang, Y., Yu, Z., 2021. Seasonal variations in biochemical composition and nutritional quality of *Crassostrea hongkongensis*, in relation to the gametogenic cycle. Food Chem. 356, 129736. https://doi.org/10.1016/j.foodchem.2021.129736.

Romo, Z.M., Re, A.D., Díaz, F., Mena, A., 2010. Physiological responses of pink abalone *Haliotis corrugata* (Gray, 1828) exposed to different combinations of temperature and salinity. Aquacult. Res. 41 (7), 953–960. https://doi.org/10.1111/j.1365-2109.2009.02377.x.

Ruiz-Feria, C.A., Beers, K.W., Kidd, M.T., Wideman, R.F., 1999. Plasma taurine levels in broilers with pulmonary hypertension syndrome induced by unilateral pulmonary artery occlusion. Poult. Sci. 78 (11), 1627–1633. https://doi.org/10.1093/ps/78.11.1627.

Sales, J., 2009. The effect of fish meal replacement by soyabean products on fish growth: a meta-analysis. Br. J. Nutr. 102 (12), 1709–1722. https://doi.org/10.1017/s0007114509991279.

Sampath, W.W.H.A., Rathnayake, R.M.D.S., Yang, M., Zhang, W., Mai, K., 2020. Roles of dietary taurine in fish nutrition. Marine Life Science & Technology 2 (4), 360–375. https://doi.org/10.1007/s42995-020-00051-1.

San, L.-Z., Liu, B.-S., Liu, B., Zhu, K.-C., Guo, L., Guo, H.-Y., Zhang, N., Jiang, S.-G., Zhang, D.-C., 2021. Genome-wide association study reveals multiple novel SNPs and putative candidate genes associated with low oxygen tolerance in golden pompano *Trachinotus ovatus* (Linnaeus 1758). Aquaculture 544, 737098. https://doi.org/10.1016/j.aquaculture.2021.737098.

Sasago, N., Takeda, M., Ohtake, T., Abe, T., Sakuma, H., Kojima, T., Sasaki, S., Uemoto, Y., 2018. Genome-wide association studies identified variants for taurine concentration in Japanese black beef. Anim. Sci. J. 89 (8), 1051–1059. https://doi.org/10.1111/asj.13030.

Shen, Y., Zhang, Y., Xiao, Q., Gan, Y., Wang, Y., Pang, G., Huang, Z., Yu, F., Luo, X., Ke, C., You, W., 2021. Distinct metabolic shifts occur during the transition between normoxia and hypoxia in the hybrid and its maternal abalone. Sci. Total Environ. 794, 148698. https://doi.org/10.1016/j.scitotenv.2021.148698.

Shi, L., Hao, G., Chen, J., Ma, S., Weng, W., 2020. Nutritional evaluation of Japanese abalone (*Haliotis discus hannai Ino*) muscle: mineral content, amino acid profile and protein digestibility. Food Res. Int. 129, 108876. https://doi.org/10.1016/j.foodres.2019.108876.

Shi, M., Yao, X., Qu, K., Liu, Y., Tan, B., Xie, S., 2023. Effects of taurine supplementation in low fishmeal diet on growth, immunity and intestinal health of *Litopenaeus vannamei*. Aquaculture Reports 32, 101713. https://doi.org/10.1016/j.aqrep.2023.101713.

Sirdah, M.M., 2015. Protective and therapeutic effectiveness of taurine in diabetes mellitus: a rationale for antioxidant supplementation. Diabetes Metab. Syndr. Clin. Res. Rev. 9 (1), 55–64. https://doi.org/10.1016/j.dsx.2014.05.001.

Stentiford, G.D., Bateman, I.J., Hinchliffe, S.J., Bass, D., Hartnell, R., Santos, E.M., Devlin, M.J., Feist, S.W., Taylor, N.G.H., Verner-Jeffreys, D.W., van Aerle, R., Peeler, E.J., Higman, W.A., Smith, L., Baines, R., Behringer, D.C., Katsiadaki, I., Froehlich, H.E., Tyler, C.R., 2020. Sustainable aquaculture through the One Health lens. Nature Food 1 (8), 468–474. https://doi.org/10.1038/s43016-020-0127-5.

Sukhavachana, S., Senanan, W., Tunkijjanukij, S., Poompuang, S., 2022. Improving genomic prediction accuracy for harvest traits in Asian seabass (*Lates calcarifer*, Bloch 1790) via marker selection. Aquaculture 550, 737851. https://doi.org/10.1016/j.aquaculture.2021.737851.

Suleria, H.A., Masci, P.P., Gobe, G.C., Osborne, S.A., 2017. Therapeutic potential of abalone and status of bioactive molecules: a comprehensive review. Crit. Rev. Food Sci. Nutr. 57 (8), 1742–1748. https://doi.org/10.1080/10408398.2015.1031726.

Sun, S.-S., Yan, L.-C., Feng, L., Jiang, W.-D., Liu, Y., Tang, L., Wu, P., Zhou, X.-Q., 2024. Taurine prevented the decline of fillet quality and muscle antioxidant capacity in on-growing grass carp (*Ctenopharyngodon idella*) fed non-fishmeal diet. Aquaculture 588, 740921. https://doi.org/10.1016/j.aquaculture.2024.740921.

Suzuki, K., Shioura, H., Yokota, S., Katoh, K., Roh, S.-G., Iida, F., Komatsu, T., Syoji, N., Sakuma, H., Yamada, S., 2017. Search for an index for the taste of Japanese black cattle beef by panel testing and chemical composition analysis. Anim. Sci. J. 88 (3), 421–432. https://doi.org/10.1111/asj.12663.

Talouarn, E., Bardou, P., Palhière, I., Oget, C., Clément, V., Tosser-Klopp, G., Rupp, R., Robert-Granié, C., 2020. Genome wide association analysis on semen volume and milk yield using different strategies of imputation to whole genome sequence in French dairy goats. BMC Genet. 21 (1), 19. https://doi.org/10.1186/s12863-020-0826-9.

Tan, K., Zhang, H., Lim, L., Zheng, H., 2020. Selection breeding program of Nan'ao Golden Scallop Chlamys nobilis with higher nutritional values and less susceptible to

stress. Aquaculture 517, 734769. https://doi.org/10.1016/j.aquaculture.2019.734769.
Vosloo, D., Vosloo, A., Morillion, E.J., Samuels, J.N., Sommer, P., 2013. Metabolic readjustment in juvenile South African abalone (*Haliotis midae*) acclimated to combinations of temperature and dissolved oxygen levels. J. Therm. Biol. 38 (7), 458–466. https://doi.org/10.1016/j.jtherbio.2013.07.001.
Wang, D., Gao, H., 2024. China Fishery Statistical Yearbook. China Agriculture Press, Beijing.
Wang, X., He, G., Mai, K., Xu, W., Zhou, H., 2016. Differential regulation of taurine biosynthesis in rainbow trout and Japanese flounder. Sci. Rep. 6, 21231. https://doi.org/10.1038/srep21231.
Wang, T., Sun, H., Zhang, M., Shen, P., Li, Y., 2024. B3GNT7 regulates mucin O-glycosylation to alleviate colonic inflammation. BMC Gastroenterol. 24 (1), 202. https://doi.org/10.1186/s12876-024-03287-8.
Wellek, S., Ziegler, A., 2009. A genotype-based approach to assessing the association between single nucleotide polymorphisms. Hum. Hered. 67 (2), 128–139. https://doi.org/10.1159/000179560.
Wu, Y., You, X., Sun, W., Xiong, G., Shi, L., Qiao, Y., Wu, W., Li, X., Wang, J., Ding, A., Wang, L., 2021. Insight into acute heat stress on meat qualities of rainbow trout (*Oncorhynchus mykiss*) during short-time transportation. Aquaculture 543, 737013. https://doi.org/10.1016/j.aquaculture.2021.737013.
Xiao, S., Yang, C., Zhang, Y., Lai, C., 2022. Downregulation of B3GNT6 is a predictor of poor outcomes in patients with colorectal cancer. World J. Surg. Oncol. 20 (1), 110. https://doi.org/10.1186/s12957-022-02561-x.
Yan, S., Zhang, M., Yang, G., Sun, Y., Ai, D., 2022. CTGF promotes the osteoblast differentiation of human periodontal ligament stem cells by positively regulating BMP2/Smad signal transduction. Biomed. Res. Int. 2022 (1), 2938015. https://doi.org/10.1155/2022/2938015.
Yin, L., Zhang, H., Tang, Z., Xu, J., Yin, D., Zhang, Z., Yuan, X., Zhu, M., Zhao, S., Li, X., Liu, X., 2021. rMVP: a memory-efficient, visualization-enhanced, and parallel-accelerated tool for genome-wide association study. Genomics Proteomics Bioinformatics 19 (4), 619–628. https://doi.org/10.1016/j.gpb.2020.10.007.
You, W., Luo, X., Ke, C., 2021. Progress in genetics and breeding of abalone. J Xiamen Univ Nat Sci 60 (2), 417–424.
Yu, F., Peng, W., Tang, B., Zhang, Y., Wang, Y., Gan, Y., Luo, X., You, W., Gwo, J.-C., Chen, N., 2021. A genome-wide association study of heat tolerance in Pacific abalone based on genome resequencing. Aquaculture 536, 736436.
Yun, B., Mai, K., Zhang, W., Xu, W., 2011. Effects of dietary cholesterol on growth performance, feed intake and cholesterol metabolism in juvenile turbot (*Scophthalmus maximus* L.) fed high plant protein diets. Aquaculture 319 (1), 105–110. https://doi.org/10.1016/j.aquaculture.2011.06.028.
Yun, B., Ai, Q., Mai, K., Xu, W., Qi, G., Luo, Y., 2012. Synergistic effects of dietary cholesterol and taurine on growth performance and cholesterol metabolism in juvenile turbot (*Scophthalmus maximus* L.) fed high plant protein diets. Aquaculture 324-325, 85–91. https://doi.org/10.1016/j.aquaculture.2011.10.012.
Zeng, J., Zhao, J., Wang, J., Bai, Y., Long, F., Deng, Y., Jiang, P., Xiao, J., Qu, A., Tong, B., Wang, M., Liu, W., Pu, F., Li, Y., Xu, P., 2023. Genetic linkage between swimming performance and disease resistance enables multitrait breeding strategies in large yellow croaker. Agriculture Communications 1 (2), 100019. https://doi.org/10.1016/j.agrcom.2023.100019.
Zhang, M., Li, M., Wang, R., Qian, Y., 2018. Effects of acute ammonia toxicity on oxidative stress, immune response and apoptosis of juvenile yellow catfish Pelteobagrus fulvidraco and the mitigation of exogenous taurine. Fish Shellfish Immunol. 79, 313–320. https://doi.org/10.1016/j.fsi.2018.05.036.
Zhang, H., Tan, K., Zheng, H., 2021. Characterization of a novel catalase gene and its response to low temperature stress in noble scallop *Chlamys nobilis* with different total carotenoids content. Aquacult. Res. 52 (12), 6179–6188. https://doi.org/10.1111/are.15479.
Zhou, X., Stephens, M., 2012. Genome-wide efficient mixed-model analysis for association studies. Nat. Genet. 44 (7), 821–824. https://doi.org/10.1038/ng.2310.
Zhou, Z., Han, K., Wu, Y., Bai, H., Ke, Q., Pu, F., Wang, Y., Xu, P., 2019. Genome-wide association study of growth and body-shape-related traits in large yellow croaker (*Larimichthys crocea*) using ddRAD sequencing. Marine Biotechnol. 21 (5), 655–670. https://doi.org/10.1007/s10126-019-09910-0.