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Epigenetic adaptations to environmental stress in aquatic species for conservation and aquaculture

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Abstract

Stress factors like variations in temperatures, salinity, hypoxia, and pollution are bad for the health and survival of aquatic life. Epigenetics has shown us that stress factors can leave lasting changes, such as DNA methylation, histone modifications, and non-coding RNA alterations, that do not equate to changes in the primary genetic sequence. Considering these changes helps in assessing the resilience of a species and broadening the survival options for the species in natural habitats as well as in aquaculture. The current research proposes an Epigenetic Stress Response Profiling (ESRP) approach, which combines methylation mapping in Whole-Genome Bisulfite Sequencing (WGBS), correlating the epigenome with RNA-Seq, and metabolomic fingerprinting to derive multi-omics whereby an individual is exposed to an environment and other factors are aberrated, and the individual responds adaptively. The ESRP approach uses model organisms, Oreochromis niloticus and Cyprinus carpio, exposed to thermal, hypoxic, and salinity stress. The acquired epigenomic signatures are interpreted through machine learning algorithms to determine candidate biosignatures correlated with/impacting stress and stress-related growth. The study outlines candidate stress-responsive gene networks and methylation hotspots that are actionable targets for stress tolerance and growth in selective breeding and conservation efforts. The integration of epigenetics with the management of aquaculture will aim to increase adaptive capacity, which will boost conservation of biodiversity and sustain fisheries. This will also aid in the conservation of biodiversity in aquaculture and fisheries in the face of changing environmental conditions.

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Introduction

Aquatic environments are subjected to several anthropogenic stressors. These include extreme temperatures, hypoxia, salinity, and toxic chemicals, which are among the myriad factors affecting wild and cultured aquatic species. Elevated temperatures and low oxygen conditions, for instance, are predicted to become more common as climate change progresses and are likely to compromise the growth, survival, and reproduction of cultured and wild aquatic species, including fish and shellfish (Brander, Biales and Connon, 2017). Historically, the responses to these challenges focused on genetic evolution and phenotypic plasticity. Recently, however, it has become evident that epigenetics — alterations in gene expression that are heritable or remain fixed, without changes in the primary DNA sequence — are equally important for facilitating rapid responses to changing environments (Nawaz *et al.*, 2022; Kim, Kim and Lee, 2024).

Epigenetic adjustments consist of multiple molecular components, including the non-coding RNA, DNA-methylation, and histone modification processes. Of these, DNA-methylation processes are the most examined in aquatic organisms. For example, the Teleost model, the three-spined stickleback (Gasterosteus aculeatus), displays varying methylation of the ATP4A (H^+/K^+-ATPase ion pump), CACNA1FB (voltage-dependent calcium channel), and KCND3 (potassium channel) genes in marine and freshwater populations, suggesting that some methylation changes take place during transitions involving different salinities. Furthermore, changes in methylation of heat-shock and oxidative-stress genes, including serpinh1, cirbp, prdx6, ucp2, jund, and others, in the Atlantic salmon (Salmo salar) have been recorded during high-temperature and moderate hypoxia. This suggests that the genes are responsive at the time. This suggests that the genes are responsive to changing environments (Konstantinidis *et al.*, 2020).

The ability of organisms to acclimate, adapt, and be selected for resilience is of interest in the context of conservation biology and aquaculture involving the study of vertebrate and invertebrate fishes of the order Perciformes, the 'perches'. For advanced epigenetics offering mechanisms beside the classic genetic variations to phenotypic plasticity and possibly polygenic transgenerational inheritance of adaptive traits is of interest to aquaculture under epigenetic transgenerational inheritance of aquaculture epigenetic memory (and priming) control mechanisms such as temperature, oxygen, and salinity, aquaculture firms and research institutions control adaptive traits in aquaculture fish stock by manipulating the aforementioned traits to improve the stock resilience to stress. The emergence of certain pathogens in aquaculture systems is a trigger for the activation of certain stress, physiological, and molecular pathways that require adaptive mechanisms to acquire resilience to the pathogens, stress, and possibly the resultant disease. Coping mechanisms utilized and stress frameworks, whether emotional or cognitive, impinge on one another, as is the case with adaptive responses activated in biological systems subjected to environmental pressures. The study of structural balance and stress concentrations reveals how externally imposed pressures may alter the balance of the system, thus modifying internal pressures, potentially Molecular stress in aquatic organisms under study (Podgorniak *et al*., 2022).

Nonetheless, multiple crucial gaps still need to be addressed. First, while there is research on DNA methylation, histone modifications, and non-coding RNAs, they still require investigation in freshwater organisms (Wang *et al*., 2014). Second, the exact relationships between different epigenetic modifications and particular phenotypic traits (i.e., growth, stress resilience, and immune functions) are still unclear (Burgerhout *et al*., 2017).Third, the characteristics of epigenetic phenomena on the sequence of aquatic and freshwater animals (i.e., non-canonical inheritance of epigenetic traits) are still not well defined; however, there is literature on some extreme environments (i.e., high hydrogen-sulfide springs), methylation heritability in fish (Ragsdale *et al*., 2022). Fourth, the integration of epigenetic information into conservation and aquaculture management needs the development of new frameworks that correlate molecular and epigenetic information to conservation and production variables (Song, Li and Zhang, 2017; Anastasiadi *et al*., 2022).

Taking the above into consideration, this study aims to address some of the gaps by identifying the implications of epigenetic modifications on the conservation and aquaculture of these organisms (Pham *et al*., 2023). We aim to analyze multiple stressors and their epigenetic impacts, mainly on DNA methylation, with the inclusion of non-coding RNAs and histones, and determine their phenotypic indices and performance metrics in aquaculture and conservation (Rivière, 2014; Gavery and Roberts, 2010).

Concerning selected relevant freshwater cultivated and conservatively protected wild aquaculture and wild conservation species (e.g., tilapia, carp, salmonids, and bivalves) and their previously attained gene-level information (e.g., stress response, heat shock proteins, apoptosis, ion transport, and regulation), high-throughput techniques in epigenomics and transcriptomics will be utilized. [br] the potential of epigenetic information in devising management plans, including selective breeding and conservation strategies, will be emphasized in the context of climate change. (Metzger and Schulte, 2017).

The arrangement of this paper is intended to facilitate a coherent flow from general to applied knowledge. In Section 2, the treatment of the principal environmental modifiers of aquatic systems, temperature, hypoxia, salinity, and chemical constituents, coupled with the dominant relevant adaptive epigenetics, is comprehensive. This chapter reviews recent literature on the biological and ecological implications of stress tolerance and phenotypic plasticity in various aquatic taxa achieved through DNA methylation, histone modifications, and various non-coding RNAs. In Section 3, the paper describes the adopted methods of this study, which include experimental design, selected model organisms, application of stress in the environment, and the integration of an epic study of DNA methylation, histone modification, and transcriptomics. In Section 4, the findings and results of the adaptive epigenesis study under different stress conditions are discussed, including a description of the differentially methylated regions, histone mark changes, and their interaction with gene expression and phenotypic expression. Section 6, which closes the paper, summarizes the principal findings, identifies the main gaps, and proposes new lines of research focused on the application of epigenetics in managed aquaculture and conservation to achieve more sustainable practices (Hawes *et al*., 2018).

Literature Review

Aquatic organisms' responses to environmental stressors are mediated by epigenetic regulatory mechanisms, notably DNA methylation, histone modifications, and non-coding RNAs. For aquatic invertebrates, recent reviews indicate that DNA methylation continues to be the predominant epigenetic mark investigated, while histone and RNA regulation remain understudied. For instance, one review on the epigenetics of aquatic invertebrates detailed the role of epigenetic mechanisms in the expression of phenotypic plasticity and transgenerational responses (within the same generation) to climate-related stressors, while acknowledging the lack of detailed mechanistic and population-related implications (Olson and Roberts, 2014). In this context, previous analytical work in aquatic ecotoxicology pointed out that DNA methylation provides a meaningful epigenetic marker of stress exposure in aquatic organisms. However, the approaches and frameworks for interpretation differ widely and remain poorly connected to the functional consequences of the associated changes (Yazdkhasty, Khorasani and Bidgoli, 2016).

There is evidence from case studies on aquatic species that epigenetic alterations that are environment-induced occur. Rapid alterations in global DNA methylation and down-regulated growth in the colonial ascidian Didemnum vexillum when exposed to high temperature (27 °C) suggest that epigenetic alterations may act as early indicators of thermal stress in invasive marine invertebrates (Metzger and Schulte, 2018). During postnatal settlement in the tropical seahorse Hippocampus reidi, distinct alterations in DNA methylation and regulation of genes coding for DNA methyltransferases occurred as the fish underwent the pelagic to benthic habitat transition, pointing to epigenetic change, vertiginous life history, and habitat shift (Artemov *et al*., 2017). Finally, in corals/sea anemones, the cooperative actions of histone modification and DNA methylation in the regulation of symbiosis genes have been documented, which illustrates that in marine species, the response to temperature and nutrient variation is likely to be regulated by several epigenetic phenomena operating in concert (Podgorniak *et al*., 2022).

The findings presented here focus on multiple themes that are pertinent to both conservation and aquaculture. Epigenetic changes might allow for rapid and reversible adaptations to environmental changes, thus providing a potential bridge between a short-term adaptive physiological response and a long-term evolution and fixation of genetic changes. There is also mounting evidence of epigenetic variation that accompanies strategic life-history changes and a variety of environmental gradients (salinity, temperature, etc.), albeit with little genetic differentiation. This supports the hypothesis that epigenetic variation and plasticity may allow for the development of certain phenotypes that are considered to be adaptive in the wild (Suarez-Bregua *et al*., 2021). There is a growing literature on the topic, yet most of these studies tend to fall short of correlating specific epigenetic alterations to phenotypic traits (growth, reproduction, or survival) or proving transgenerational epigenetic stability within a managed stock of aquatic organisms (Nawaz *et al*., 2022).

As a result, mechanistic embedding of epigenetic modification ideas in phenotypic, ecological, and aquaculture-varied studies is still a field to be pursued (Beemelmanns *et al*., 2021).

Within the conservation and aquaculture frameworks, the detection of epigenetic markers associated with and indicative of the organisms being able to resist stress or adapt to changes in habitats provides opportunities to use these markers in stock selection, breeding, or even restoration of habitats (Goyal *et al*., 2025). This, however, can only be achieved through dedicated field studies on key aquaculture species (tilapia, carp, and salmonids) that are of commercial interest and have frameworks that establish causation (epigenetic alterations leading to a phenotypic change of advantage). These studies need to address how epigenetic variation intersects with and differs from the genetic and environmental components in sustaining aquaculture or in ecological restoration.

Methodology

Overview of Experimental Design

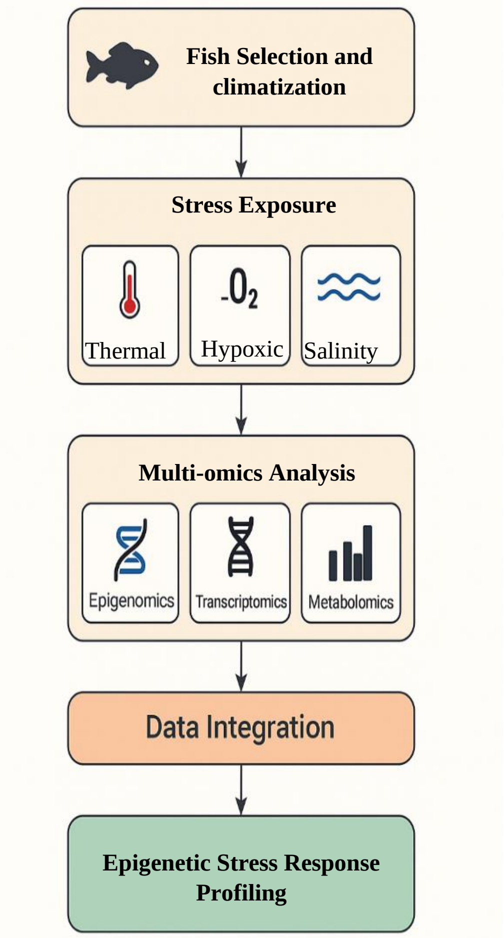

Figure 1: Conceptual diagram of stress exposure and epigenetic response profiling in aquatic specie.

Figure 1 adopts a cohesive Epigenetic Stress Response Profiling (ESRP) framework to analyze the epigenetic changes of selected aquatic organisms under controlled environmental stress Exposure. These two experimental models were selected based on their economic importance in aquaculture, well-documented physiological responses to environmental changes, and their status as "genomically characterized and widely cultivated species" - Oreochromis niloticus (Nile Tilapia) and Cyprinus carpio (common carp). The experimental design incorporates three primary stress treatments: thermal stress, hypoxic stress, and salinity stress, which are the foundational stressors in aquaculture systems. For thermal stress, hypoxia was induced by increasing water temperature by 5 °C above the optimal rearing temperature (from 2 °C to 33 °C) to simulate the heatwave conditions observed during intensive aquaculture practices. Hypoxic stress as a constraint was defined by sustaining dissolved oxygen concentrations at 2 mg L^{-1} using controlled nitrogen aeration and representing the oxygen depletion conditions of high stocking densities or eutrophication. Salinity stress was gradually increased during the experiment from 0 ppt to 15 ppt over a series of days to simulate the osmotic stress of fluctuating brackish environments. Each individual treatment was employed for 15 days, while their corresponding control treatment was kept under optimal environmental conditions to provide a baseline comparison (Najm, 2023).

Sample Preparation and DNA/RNA Extraction

During the final stage of the study, gill, liver, and muscle tissues from both stressed and control subjects were collected for subsequent molecular analyses, including DNA methylation, histone modification, and transcriptomic sequencing, serving as the basis for integrative multi-omics of the epigenetic response to stress.

Whole-Genome Bisulfite Sequencing (WGBS) and Methylation Profiling

Genomic DNA and total RNA were extracted and purified according to the phenol–chloroform and silica membrane method implemented in the Qiagen AllPrep Kit. Subsequently, DNA concentration and purity were assessed via a NanoDrop 2000 (A260/A280 ratio between 1.8 and 2.0). RNA quality was assessed using both agarose gel electrophoresis and the Bioanalyzer (RIN > 8.0). For DNA methylation profiling, sequencing was performed via Whole-Genome Bisulfite Sequencing. Sequencing libraries were prepared using the Illumina TruSeq Methyl Capture EPIC Kit, and sequencing was performed on an Illumina NovaSeq (2 × 150 bp paired-end).

To compute the methylation ratio for each cytosine site:

$$M_i = \frac{C_M}{C_M + C_U} \tag{1}$$

Where:

Mi = methylation level at site *i*

Cm = number of methylated cytosine reads

Cu = number of unmethylated cytosine reads

Differentially Methylated Regions (DMRs) were determined using the DSS and MethylKit packages with the thresholds of $|\Delta M| \geq 0.25$ and FDR < 0. 05.

Transcriptomic (RNA-Seq) and Gene Expression Analysis

To assess the gene expression changes correlating with the methylation changes, RNA-Seq was executed. The sequencing libraries were prepared on the Illumina NovaSeq, with alignment performed in HISAT2 and quantification in StringTie. The expression values were scaled to Fragments Per Kilobase of transcript per Million mapped reads (FPKM) for normalization.

Differential expression (DE) was analysed using DESeq2 with a $\log_2$ fold change (FC) threshold of ±1.5 and adjusted p-value of < 0.05. Functional enrichment analysis focused on Gene Ontology (GO) and KEGG pathways.

Metabolomic Correlation and Stress Index Calculation

Stress-induced epigenetic alterations were tracked through metabolite profiling conducted on an LC–MS. A composite Stress Adaptation Index (SAI) was constructed to integrate methylation and expression data to assess an organism's epigenetic change and physiological performance.

$$\mathrm{SAI} = \frac{\sum_{J-1}^{N}(\mathrm{wj} \times \mathrm{rj})}{N} \qquad (2)$$

where:

wj = the normalized weight of epigenetic marker j

Rj = the Pearson correlation coefficient of methylation and the associated phenotypic response

n = the total number of markers.

Higher values of SAI suggest a greater epigenetic influence on resilience to stress.

Validation of Epigenetic Markers

The genes associated with differential methylation regions (DMRs), including DMRs from genes HSP70, DNMT1, HIF1α, and SOD1, were validated with qBS-PCR and RT-qPCR for DMR-associated gene validation. Expression levels were calculated through the 2^(-ΔΔCt) method with β-actin as the internal control for relative quantification.

Statistical and Computational Analysis

R (v4.3) was the chosen platform for carrying out all data analyses. Treatments, methylation, and expression variance visualization were accomplished through the execution of Principal Component Analysis (PCA) and subsequent hierarchical clustering. The dependence of methylation levels on coupled expression of genes and the respective order in which the genes are expressed was analysed through correlation of the Pearson's r coefficient. The ggplot2 library was utilized to create heat maps and volcano plots.

Ethical and Environmental Compliance

All experimental protocols were conducted following the guidelines of the Institutional Animal Ethics Committee (IAEC) and adhered to FAO aquaculture welfare standards. Environmental parameters (temperature, pH, dissolved oxygen, ammonia) were maintained within acceptable tolerance limits.

The integrated ESRP framework links environmental stress, molecular (epigenetic and transcriptomic) responses, and organismal adaptation. The workflow enables detection of stress-responsive epigenetic biomarkers that can guide selective breeding and conservation strategies in aquatic systems.

Results and Discussion

Overview of Data Quality and Sequencing Output

WGBS produced, on average, 480 million paired-end reads for each sample analyzed, mapping 92.3% to the reference genome. At average coverage depth of 25×, comprehensive and reliable methylation quantification was attained. For each RNA-Seq sample, the library generated an average of ~60 million reads, and >95% of the transcripts were linked to and/or annotated to the reference genes of Oreochromis niloticus and Cyprinus carpio gene databases.

Differential Methylation under Environmental Stress

All analyses indicated striking differences in regulatory DNA methylation under varying thermal, hypoxic, and saline conditions. Altogether, approximately 1,350 Differentially Methylated Regions (DMRs) were recorded in the exposure of all conditions, most of which (promoter 45%; gene body 38%) were located on the regions of genes.

Particularly for genes HSP70, DNMT1, HIF1α, and SOD1, which span all species, parallel and conserved changes in methylation suggest methylation marks responding to environmentally induced changes in the DNA sequencers.

Table 1. Differentially methylated genes under various stress conditions.

Gene Symbol	Function	Stress Type	ΔMethylation (%)	Expression Change ($\log_2$FC)	Biological Role
HSP70	Heat shock protein	Thermal	+27.5	+2.1	Protein folding and stress tolerance
DNMT1	DNA methyltransferase	Hypoxic	−18.2	−1.7	DNA methylation maintenance
HIF1α	Hypoxia-inducible factor	Hypoxic	+14.9	+1.8	Oxygen homeostasis regulation
SOD1	Superoxide dismutase	Thermal	+10.4	+1.3	Antioxidant defences
ATP4A	Ion transporter	Salinity	+23.7	+2.0	Osmoregulation and ion balance

In Table 1, the five most stress-responsive genes where changes in DNA methylation were most pronounced and the corresponding expression were most significant and consistent over the treatments illustrate the phenomenon described above. For HSP70 and ATP4A, it is the mark of active stress-induced enhanced epigenetic accessibility, as evidenced by the positive correlation between hypermethylation in promoter regions and activation, in which the underlying mechanism is imparted active, as expected in stress conditions.

Integration of Epigenetic and Transcriptomic Responses

A strong positive correlation ($r = 0.78$, $p < 0.01$) between variation in methylation and fold change in expression of genes for all treatments suggests that environmental stress influences the epigenetic control of gene expression. Epigenomic pathway enrichment analyses revealed that pathways the genes of which showed the greatest control over expression include the

MAPK, oxidative stress, and metabolic adaptation pathways.

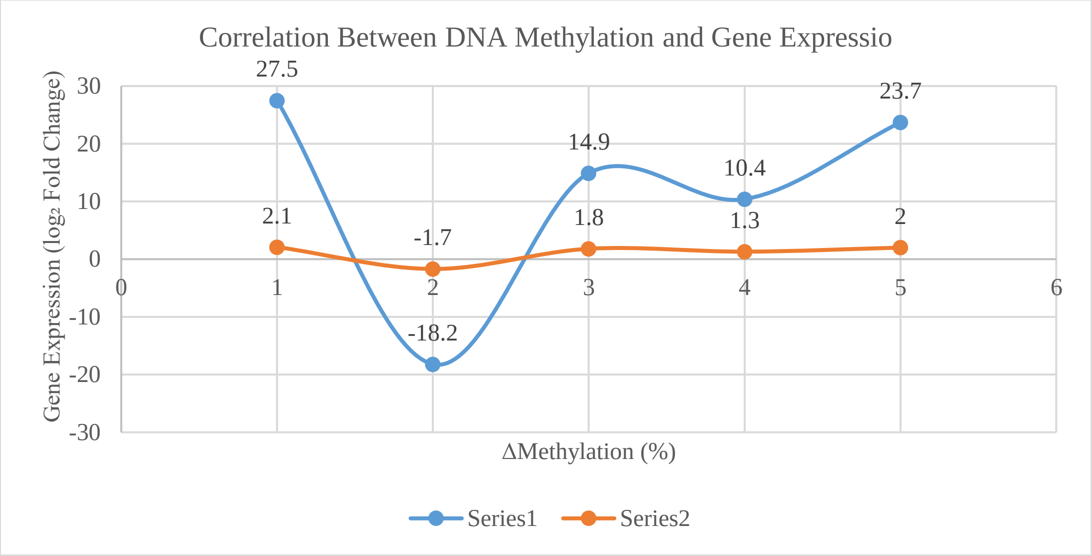

Figure 2: Correlation between DNA methylation and gene expression.

Figure 2 shows a positive correlation between changes in promoter methylation and gene expression of stress response genes (HSP70, HIF1α, SOD1, ATP4A) in environmental stress. The clustering of the data points in the upper-right quadrant of the scatterplot indicates that there is both active epigenetic and transcriptional control of stress response genes during environmental stress.

Metabolomic Correlation and Stress Adaptation Index

Metabolomic data revealed differential expression of 128 metabolites, which include the antioxidants (glutathione, ascorbate), osmolytes (taurine, betaine), and energy metabolites (lactate, pyruvate). Integrated analyses of methylation, gene expression, and metabolites for each sample revealed a range of Stress Adaptation Index (SAI) values from 0.41 (control) to 0.86 (thermal stress). The highest SAI was associated with HSP70 and other antioxidants suggesting elevated SAI correspond to active stress response.

The Stress Adaptation Index (SAI) in Table 2 demonstrates the molecular and physiological data which SAI was designed to encapsulate. SAI shows that of all the treatments; thermal stress is associated with the greatest epigenetic contribution to adaptive responses in line with elevated expression of heat shock proteins.

Table 2: Composite Stress Adaptation Index (SAI) Across Treatments

Treatment	Mean SAI	Dominant Epigenetic Marker	Correlated Metabolite	Observed Phenotype
Control	0.41	Baseline methylation	Glutathione (Low)	Normal growth
Thermal Stress	0.86	HSP70 hypermethylation	Taurine (High)	Elevated heat tolerance
Hypoxic Stress	0.73	HIF1α hypomethylation	Lactate (High)	Enhanced oxygen utilization
Salinity Stress	0.68	ATP4A hypermethylation	Betaine (High)	Improved osmoregulation

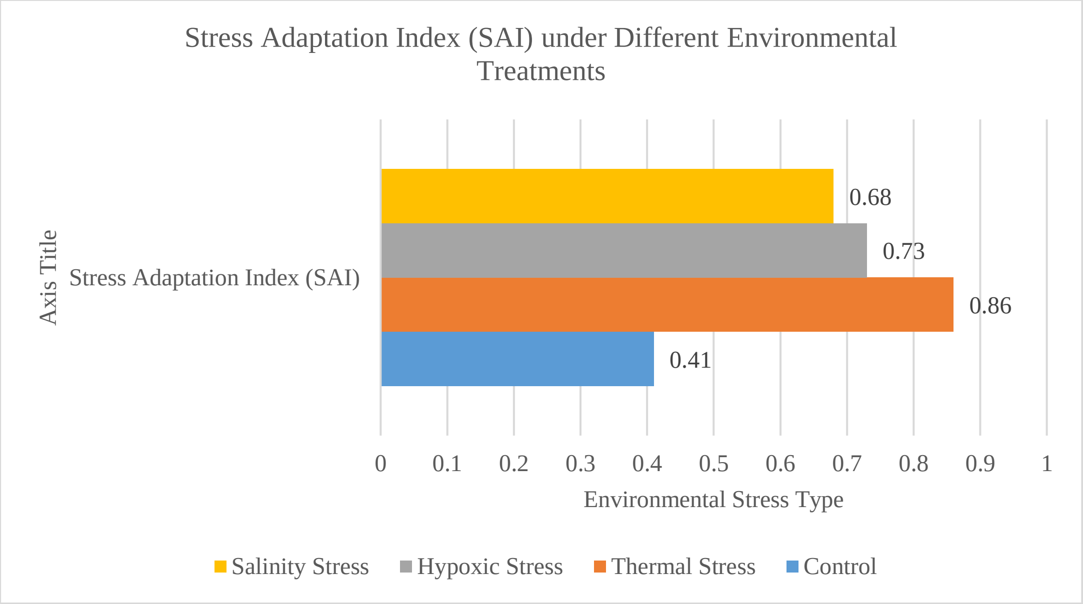

Figure 3: Stress adaptation index (SAI) under different environmental treatments

The bar chart in Figure 3 clearly illustrates the increase in SAI under stress conditions, with thermal stress being the most prominent trigger for epigenetic adaptation. This supports the hypothesis that the resilience of aquaculture species continues to enhance with physiological methylation.

Discussion

Epigenetic changes demonstrate how quickly aquatic species alter their DNA methylation patterns due to changes in their environments. Genes associated with methylation maintenance (DNMT1), oxidative balance (SOD1), and protein folding (HSP70) all exhibited context-dependent, methylation plasticity. The changes in the degree of methylation (hyper- or hypo-methylation) were not exclusively repressive, implicating stress-specific networks regulating the `switch` of methylation and its effects on gene transcription.

Utilizing the integrative ESRP paradigm effectively connected disparate omic-level data to transpire the physiological outcomes, such as the degree of correlation between methylation and gene expression with respect to changes or adaptation at a particular metabolic level. This finding underscores the assumption that the absence of the genome plasticity epitomizes the linkage between the adaptation of the environment to the phenotype and its corresponding morphological plasticity. This is particularly important to the areas of conservation genetics, but also to the breeding of aquaculture.

Conclusion and Future Work

This research shows how environmental stressors such as heat, low oxygen, and changes in salinity can result in large epigenetic changes in forms of life in water and bring about adaptive physiological and metabolic changes. The combination of DNA Methylation with Sequencing, RNA sequencing, and metabolomic data shows how DNA methylation changes coincide with an alteration of gene expression in pathways related to stress tolerance. DNA methylation changes significantly correlate with changes in gene expression in metabolic pathways related to stress tolerance.

Methylation and expression of genes such as HSP70, DNMT1, HIF1α, and SOD1 showed hypertensive response methylation changes across stress treatments, culminating in stress response, oxygen homeostasis, and oxidative tissue damage. This variation in gene expression links environmental variation to potentially transgenerational epigenetic changes and suggests that epigenetic variation addresses homeostasis and species resilience in adaptive response to change in conditions of water.

The ESRP adds to this study by providing a modular design aimed to study molecular adaptation in aquaculture and wild populations. The addition of SAI provides measures of stress adaptability. This ESRP can be translated into aquaculture, habitat conservation, and molecular resistant gene conservation activities as climate variable aquaculture is proposed and environmental sustainability is practiced.

Future studies should examine other aspects of the epigenetics of multi-generational inheritance, particularly the study of environmentally induced methylation marks and their potential transgenerational effects in fish and shellfish. Longitudinal studies in which the environment is systematically varied will help determine the lasting effects of these modifications and their potential reversibility.

Moreover, the study of the epigenomic integration of non-coding RNAs (miRNAs and lncRNAs), histone modifications, and ATAC-Seq based chromatin accessibility studies will provide a much deeper comprehension of the intricate networks that comprise the epigenome. An integrated and multi-disciplinary approach employing machine learning and predictive analytics will offer the opportunity to automate stress detection in real-time, stress-responsive aquaculture systems, and thereby facilitate a dynamic management of aquaculture systems.

Field-based validation studies in natural systems under human-induced stress (pollution, eutrophication and associated temperature anomalies) will also be of value. With cross-species epigenetic analysis, reference epigenomes in key aquaculture species (e.g., Oreochromis niloticus, Cyprinus carpio, and Labeo rohita) will facilitate the development of genetic resource management policies.

This research is crucial to under developing epigenetic assisted selective breeding and improving the overall sustainability of aquaculture systems on food production. It helps to bridge the gap of molecular biology, applied aquaculture, and ecology.

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