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Mechanisms of Adaptation in Aquatic Species: From Phenotypic Plasticity to Genetic Evolution

Rudi Mai
Tropical Marine Fisheries Research Center, Hainan Institute of Tropical Agricultural Resources, Sanya, 572025, Hainan, China
Corresponding email: rudi.mai@hitar.org

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Abstract This study explores the mechanisms of adaptation in aquatic species, including phenotypic plasticity, genetic evolution, and molecular mechanisms. Aquatic species exhibit significant phenotypic plasticity, allowing them to respond rapidly to environmental changes. Changes in gene expression related to osmoregulation and metabolic processes demonstrate how species adjust their physiological states to cope with varying conditions. Genetic evolution plays a crucial role in long-term adaptation, driven by processes such as mutation, natural selection, and genetic drift. Research shows that specific genes in marine mammals and freshwater prawns are crucial for their adaptation to aquatic environments. Molecular adaptations involve gene regulation, genomic changes, and epigenetic modifications. Studies on fireflies and marine diatoms provide insights into the genetic basis of adaptation to different environmental conditions.

Keywords Phenotypic plasticity; Genetic evolution; Gene expression; Aquatic species; Adaptation mechanisms

1 Introduction

Aquatic species exhibit a diverse array of adaptations that enable them to survive and thrive in various water environments. These adaptations, which can be physiological, morphological, or behavioral, are essential for overcoming the unique challenges posed by aquatic habitats. This research delves into the mechanisms of adaptation in aquatic species, exploring both phenotypic plasticity and genetic evolution.

Adaptation in aquatic species involves a variety of changes that allow organisms to cope with the specific demands of living in water. These changes include modifications in osmoregulation, respiration, locomotion, and sensory systems. For instance, secondary aquatic vertebrates, which have transitioned from terrestrial to aquatic environments, have developed numerous convergent adaptations such as changes in body shape, buoyancy control, and enhanced respiratory and sensory capabilities (Houssaye and Fish, 2016). The adaptation process can be seen in various species, such as marine mammals, which have evolved specific physiological traits to survive in marine environments. These traits include the ability to dive deep and remain submerged for extended periods, modifications in the structure and function of the respiratory system, and enhanced sensory systems for navigating and hunting in the aquatic environment (Davis, 2019).

Plants also exhibit significant adaptations when transitioning from terrestrial to aquatic habitats. For example, the aquatic plant *Ranunculus bungei* and its terrestrial relatives have shown molecular adaptations in genes related to water transport and microtubule organization, which are crucial for survival in submerged conditions (Chen et al., 2015). Similarly, fireflies that have both terrestrial and aquatic larvae have demonstrated genetic adaptations that enhance their metabolic efficiency and morphology for aquatic living (Zhang et al., 2020).

Understanding the mechanisms of adaptation in aquatic species is crucial for several reasons. First, it provides insights into the evolutionary processes that shape biodiversity. Studying these mechanisms can reveal how different species have independently evolved similar solutions to common environmental challenges. This knowledge helps us understand the broader principles of evolution and adaptation. For example, the study of fireflies has revealed significant differences in gene expression related to metabolic efficiency and hypoxia response between aquatic and terrestrial species, highlighting the role of genetic evolution in adaptation (Yang et al., 2022).

Additionally, knowledge of these adaptations can inform conservation strategies, particularly as aquatic environments face increasing threats from climate change and human activities. Changes in climate and increased pollution can alter the habitats and survival conditions of aquatic species, making it essential to understand how these organisms adapt to changing conditions. For instance, marine species have been observed to shift their distributions and timing of biological events as a response to climate change, but evidence for adaptation through evolutionary processes remains limited (Miller et al., 2018). Understanding these adaptation mechanisms can guide the development of effective conservation and management strategies to protect aquatic biodiversity.

This study provides a comprehensive overview of the various types of adaptations observed in aquatic species. It will delve into the molecular and genetic bases of these adaptations, exploring how these mechanisms contribute to the survival and fitness of aquatic species in their environments. Additionally, the study will discuss the implications of these adaptations in the context of environmental changes and human impacts. By highlighting recent advances in research, this study aims to deepen the understanding of the adaptive strategies employed by aquatic species to thrive in their habitats.

2 Phenotypic Plasticity

2.1 Definition and examples

Phenotypic plasticity is the ability of an organism to alter its phenotype in response to changes in the environment. This section explores the definition, mechanisms, and role of phenotypic plasticity in short-term adaptation, with examples from various aquatic species.

Phenotypic plasticity refers to the capacity of a single genotype to produce different phenotypes under varying environmental conditions. This adaptive flexibility can manifest in morphological, physiological, behavioral, or developmental changes, allowing organisms to better survive and reproduce in fluctuating environments. For instance, amphibious fishes exhibit significant plasticity in their ability to adapt to both terrestrial and aquatic habitats. These adaptations include changes in buoyancy control, hydration mechanisms, and respiratory function, enabling them to survive both in water and on land (Wright and Turko, 2016). Similarly, aquatic plants like Elodea nuttallii show extensive plasticity in response to varying light and nitrogen levels, which contributes to their invasive success in different water bodies (Szabó et al., 2018).

2.2 Mechanisms of phenotypic plasticity

The mechanisms underlying phenotypic plasticity involve a complex interplay of genetic, molecular, and environmental factors. At the genetic level, plasticity often relies on regulatory genes that can modulate the expression of other genes in response to environmental cues. For example, the freshwater snail *Radix balthica* exhibits predator-induced plasticity in shell shape, driven by differential gene expression in response to the presence of predators (Hollander et al., 2017). Molecularly, these responses can involve changes in hormone levels, enzyme activities, and cellular signaling pathways that facilitate rapid phenotypic adjustments. In amphibious fishes, phenotypic plasticity allows for adjustments in metabolic processes and ion transport mechanisms, enabling them to cope with the distinct challenges of terrestrial and aquatic environments (Wright and Turko, 2016).

Phenotypic plasticity also operates through developmental plasticity, where environmental conditions experienced during early life stages can influence the developmental trajectory of an organism. This is evident in frog tadpoles, which can alter their growth, development, and behavior in response to the presence of predators, enhancing their survival prospects in predator-rich environments (Van Buskirk, 2017).

2.3 Role in short-term adaptation

Phenotypic plasticity plays a crucial role in the short-term adaptation of aquatic species to rapidly changing environments. By enabling immediate and reversible changes in phenotype, plasticity allows organisms to maintain functionality and fitness across a range of environmental conditions. This adaptive capacity is particularly important in environments that experience frequent and unpredictable changes, such as fluctuating water levels, temperature shifts, and variations in nutrient availability.

For example, the plastic responses of amphibious fishes to terrestrial and aquatic environments not only facilitate their survival but also provide insights into the evolutionary processes that may have enabled the transition of vertebrates from water to land (Wright and Turko, 2016). In aquatic plants, phenotypic plasticity in traits such as growth form, root length, and branching patterns allows them to exploit different ecological niches and compete effectively with other species (Szabó et al., 2018).

Moreover, phenotypic plasticity can buffer populations against environmental stressors, potentially providing a temporary adaptive advantage while genetic adaptation catches up. This buffering effect is crucial in the context of global environmental changes, such as climate change, which impose new selection pressures on aquatic ecosystems (Gibbin et al., 2017). The ability to rapidly adjust phenotypes in response to these changes can enhance the resilience of populations and ecosystems, promoting stability and persistence in the face of environmental perturbations.

3 Genetic Evolution

3.1 Definition and processes

Genetic evolution is a fundamental process that drives the adaptation of species to their environments through changes in their genetic makeup over generations. This section will discuss the definition and processes of genetic evolution, the roles of natural selection and genetic drift, and the significance of genetic evolution in long-term adaptation.

Genetic evolution refers to changes in the frequency of alleles (different versions of a gene) within a population over time. These changes result from various processes including mutation, gene flow, genetic drift, and natural selection. Mutations are random changes in the DNA sequence that can introduce new genetic variations. Gene flow occurs when individuals migrate between populations, bringing new alleles into a population. Genetic drift is the random fluctuation of allele frequencies from one generation to the next, which can have significant effects in small populations. Natural selection is the process by which certain traits become more common in a population because they confer a survival or reproductive advantage (Foote et al., 2015).

The combination of these processes leads to genetic diversity within populations, which is crucial for adaptation to changing environments. For instance, in the aquatic firefly, genetic adaptations to freshwater environments involve significant changes in genes related to metabolic efficiency and hypoxia response (Zhang et al., 2020).

3.2 Natural selection and genetic drift

Natural selection and genetic drift are two primary mechanisms that drive genetic evolution. Natural selection acts on phenotypic variation, favoring traits that enhance an organism’s fitness in its environment. For example, marine mammals such as whales and dolphins have evolved specific adaptations for thermoregulation and deep diving, driven by positive selection on genes involved in these traits (Yuan et al., 2021).

Genetic drift, on the other hand, refers to random changes in allele frequencies that can lead to significant genetic differences between populations, particularly in small or isolated populations. This stochastic process can result in the loss of genetic variation and the fixation of alleles. In freshwater snails, genetic drift has been shown to influence the evolution of phenotypic plasticity, with high rates of gene flow necessary to maintain genetic diversity (Hollander et al., 2017).

3.3 Role in long-term adaptation

Genetic evolution plays a critical role in the long-term adaptation of species to their environments. Over extended periods, genetic changes accumulate, leading to the emergence of new species and the development of complex adaptations. The study of aquatic vertebrates, for instance, reveals how genomic changes have facilitated their adaptation to aquatic life. For example, the genomes of marine mammals exhibit convergent evolution, with similar genetic changes occurring independently in different lineages to adapt to aquatic environments (Foote et al., 2015).

The genomic adaptations in aquatic insects also highlight the role of genetic evolution in long-term adaptation. For example, fireflies that transitioned to freshwater habitats have undergone significant genomic changes that enhance their metabolic efficiency and morphological adaptations (Zhang et al., 2020).

Moreover, the adaptation of aquatic plants through genetic evolution has been crucial for their survival and proliferation in diverse aquatic habitats. The genomic analysis of aquatic angiosperms like those in the Alismatales order reveals how whole-genome duplications and gene losses have facilitated their adaptation to both freshwater and marine environments (Chen et al., 2022).

4 Molecular Mechanisms of Adaptation

4.1 Gene regulation and expression

Adaptation at the molecular level involves various mechanisms that enable organisms to survive and thrive in changing environments. These mechanisms include gene regulation and expression, genomic changes and mutations, and epigenetic modifications. This section explores each of these mechanisms and their roles in the adaptation of aquatic species.

Gene regulation and expression play a crucial role in how organisms respond to environmental changes. Regulatory mechanisms control the timing, location, and amount of gene expression, allowing organisms to adapt to different environmental conditions. For instance, in the freshwater firefly species *Aquatica leii*, differential gene expression patterns have been observed between aquatic larvae and terrestrial adults. These patterns are primarily associated with metabolic efficiency, energy production, and hypoxia response, which are essential for adapting to freshwater environments (Zhang et al., 2020).

The transcriptome sequencing of *Ranunculus bungei*, an aquatic plant, and its terrestrial relatives revealed that genes involved in water transport and microtubule cytoskeleton organization are differentially expressed in response to aquatic habitats. These genes help the plant adjust its physiology to cope with submerged conditions (Chen et al., 2015). Similarly, the molecular adaptation mechanisms in cetaceans include the regulation of genes involved in body shape changes, osmotic regulation, immune defense, dietary changes, sensory systems, and hypoxic tolerance, reflecting the complex genetic adjustments required for a secondary aquatic life (Yang et al., 2019).

4.2 Genomic changes and mutations

Genomic changes and mutations are fundamental to the evolutionary adaptation of species. Mutations introduce genetic variation, which natural selection can act upon. In the case of aquatic adaptations, specific genes often undergo positive selection, leading to advantageous traits that enhance survival in aquatic environments. For example, comparative genomic studies on marine mammals have identified genes related to thermoregulation, such as those involved in the formation of blubber and vascular development, which have undergone unique changes to adapt to marine life (Yuan et al., 2021).

The molecular basis of freshwater adaptation in fireflies also includes fast-evolving genes and positively selected genes that contribute to metabolic efficiency and morphological adaptations. These genetic changes are essential for the fireflies to cope with the challenges of freshwater habitats (Zhang et al., 2020). In another example, the freshwater adaptation in prawns of the genus Macrobrachium involves differential gene expression and positive selection in genes related to osmoregulation, hemolymph regulation, and stress response, facilitating their survival in varying salinity conditions (Rahi et al., 2019).

4.3 Epigenetic modifications

Epigenetic modifications, such as DNA methylation and histone modifications, play a significant role in regulating gene expression without altering the underlying DNA sequence. These modifications can be influenced by environmental factors and can provide a rapid and reversible means of adaptation. In aquatic species, epigenetic changes can help organisms respond to environmental stresses, such as changes in salinity, temperature, and oxygen availability.

For instance, in the marine diatoms, temperature acclimation involves changes in gene expression regulated by epigenetic mechanisms. These changes help diatoms adjust their metabolic processes to cope with different thermal environments (Liang et al., 2019). Epigenetic modifications also contribute to the adaptation of fish to salinity changes, where specific genes involved in ion transport and osmoregulation are differentially methylated in response to salinity stress (Xu et al., 2015).

5 Environmental Factors Influencing Adaptation

5.1 Temperature and climate change

Environmental factors play a significant role in shaping the adaptive mechanisms of aquatic species. These factors include temperature and climate change, salinity and water chemistry, and habitat complexity and availability. This section explores how these factors influence adaptation in aquatic organisms. Temperature is a critical environmental factor that influences the physiology, behavior, and distribution of aquatic species. Climate change, characterized by global warming, has significant impacts on aquatic ecosystems, altering the temperature regimes of water bodies and affecting the species that inhabit them. Aquatic species must adapt to these changes to survive and maintain their ecological roles.

For instance, a study on marine diatoms (*Thalassiosira pseudonana*) demonstrated rapid thermal adaptation over 350 generations, showing significant divergence in temperature response traits. This adaptation highlights the ability of microorganisms to evolve rapidly in response to temperature changes, which is crucial for their survival in warming oceans (O'Donnell et al., 2018). Similarly, bivalve mollusks like *Unio tumidus* exhibit adaptive reactions to temperature changes, modulating their metabolic processes to cope with increased water temperatures (Krasyuk and Khudiyash, 2021).

Climate change also interacts with other environmental stressors, compounding their effects on aquatic species. For example, the combination of increased temperatures and pollution can lead to novel stress conditions that require complex adaptive responses from aquatic organisms (Niinemets et al., 2017).

5.2 Salinity and water chemistry

Salinity and water chemistry are crucial factors affecting the distribution and adaptation of aquatic species. Changes in salinity levels can result from natural processes or human activities, such as the discharge of industrial effluents and the use of road salts. Aquatic species must adapt to varying salinity levels to maintain osmotic balance and other physiological functions.

Research on the Gulf killifish (*Fundulus grandis*) has shown that populations in polluted habitats have rapidly evolved resistance to high levels of salinity. This adaptation involves genomic changes related to osmoregulation and ion transport, enabling the fish to survive in highly saline environments (Oziolor et al., 2019) (Figure 2). Similarly, studies on freshwater macroinvertebrates, such as the flatworm Dugesia gonocephala, have identified loci associated with adaptation to high copper concentrations from ore mining, indicating a genetic basis for local adaptation to specific water chemistry conditions (Weigand et al., 2018).

Epigenetic mechanisms also play a role in salinity adaptation. For instance, changes in DNA methylation patterns have been observed in fish adapting to different salinity levels, influencing the expression of genes involved in ion transport and stress response (Xu et al., 2015).

Figure 1 illustrates the variation in sensitivity to pollution among different populations of F. grandis in Galveston Bay, USA. The main content is as follows: (A) Pollution gradient map: Different colors represent pollution levels, ranging from low (blue) to high (black). Populations are classified based on their pollution resistance into four categories: highly resistant (black), intermediate-high resistance (red), intermediate-low resistance (yellow), and sensitive (blue). (B) Cardiac deformities in embryos: This shows the degree of heart deformities in different populations when exposed to PCB126. The results indicate that populations from highly polluted areas have stronger resistance to PCB126, while those from less polluted areas are more sensitive. (C) EC50 and pollution correlation: This shows the positive correlation between the sensitivity of populations to PCB126 (EC50) and the pollution level of their habitats. (D) CYP1A activity and pollution correlation: This shows the negative correlation between the maximum CYP1A activity of populations and their sensitivity to PCB126. (E) Variation in CYP1A activity: This shows the variation in PCB126-induced CYP1A activity among individuals and populations. Overall, Figure 1 demonstrates the differences in pollution resistance among F. grandis populations at different pollution levels and reveals the correlation between these differences and the inducibility of CYP1A enzyme activity (Adapted from Oziolor et al., 2019).

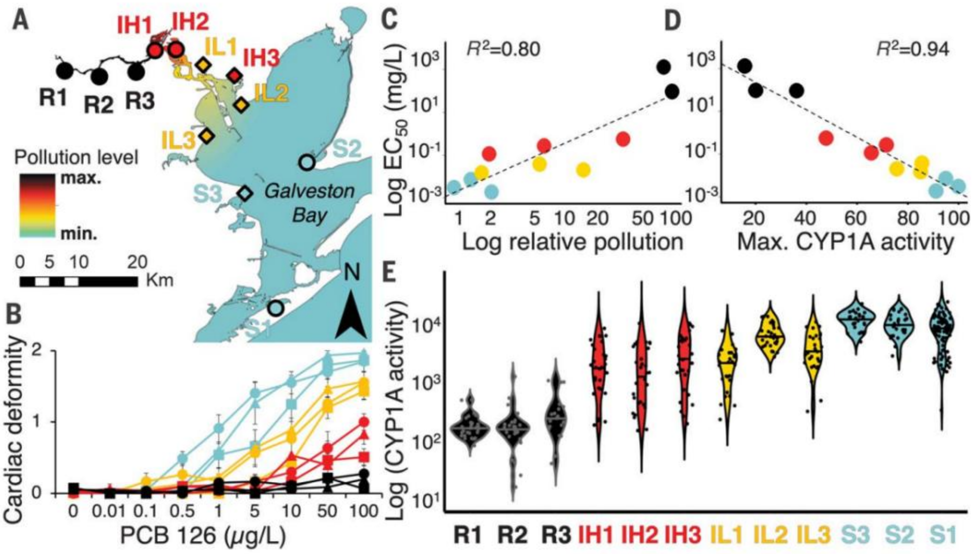

Figure 1 Variation in sensitivity to pollution among *F. grandis* populations distributed along a steep pollution gradient in Galveston Bay (USA) (Adopted from Oziolor et al., 2019)

Image caption: (A)Pollution gradient is scaled by color, from low (blue) to high (black). Populations include resistant (black, R1 to R3), intermediate-high resistance (red, IH1 to IH3), intermediate-low resistance (gold, IL1 to IL3), and sensitive (blue, S1 to S3). Genomics data were collected for populations denoted with circles. (B) Population variation in cardiac deformities in embryos exposed to PCB126 (error bars indicate standard error of the mean). Population variation in sensitivity to PCB-induced cardiac deformities [log median effective concentration (EC50)] correlates with (C) habitat pollution and (D) AHR pathway inducibility (CYP1A activation by PCB126). (E) PCB-induced CYP1A activity varies among individuals and populations (Adopted from Oziolor et al., 2019).

5.3 Habitat complexity and availability

Habitat complexity and availability are vital for the survival and adaptation of aquatic species. The structural characteristics of aquatic habitats, such as the presence of vegetation, substrate type, and water flow, influence the ecological niches available to species and their adaptive strategies.

Aquatic insects, for example, exhibit various adaptations to different water flow regimes in streams. Species adapted to high-velocity riffles and low-velocity pools show distinct morphological and behavioral traits that enable them to cope with the specific challenges of their habitats. These adaptations include changes in body shape and drifting behavior, which are crucial for maintaining position and accessing resources in flowing water (Mazzucco et al., 2015).

The availability of suitable habitats is also influenced by human activities, such as habitat destruction and pollution, which can reduce the complexity and quality of aquatic environments. Conservation efforts must consider these factors to preserve the adaptive potential and biodiversity of aquatic species.

6 Case Studies of Adaptation in Aquatic Species

6.1 Adaptation in marine species

The study of adaptation in aquatic species provides valuable insights into how organisms adjust to their environments through a combination of phenotypic plasticity, genetic evolution, and molecular mechanisms. This section presents detailed case studies on adaptation in marine and freshwater species, followed by a comparative analysis.

Marine species exhibit a range of adaptive strategies to survive in their dynamic and often harsh environments. One notable example is the adaptation of marine diatoms, such as *Thalassiosira pseudonana*, to varying temperatures. Research has shown that these diatoms can rapidly evolve thermal tolerance, demonstrating significant divergence in temperature response traits over 350 generations. This rapid thermal adaptation involves trade-offs that affect their physiological and ecological performance, highlighting the ability of microorganisms to adjust swiftly to climate change (O'Donnell et al., 2018).

Another significant case study is the adaptation of marine mammals, such as cetaceans. Genomic analyses have revealed that cetaceans have undergone extensive genetic changes to adapt to their aquatic lifestyle. These adaptations include modifications in genes related to hypoxia tolerance, lipid metabolism, and sensory functions. The transition from land to water in these species involved positive selection on numerous genes, allowing them to thrive in the marine environment (Tsagkogeorga et al., 2015).

Marine species also adapt to changing salinity levels. For example, the Gulf killifish (*Fundulus grandis*) has developed resistance to extreme salinity through genomic changes that enhance osmoregulation. This adaptation is crucial for survival in highly saline environments, demonstrating the importance of genetic evolution in coping with environmental stressors (Oziolor et al., 2019).

6.2 Adaptation in freshwater species

Freshwater species face different adaptive challenges compared to their marine counterparts. The Tibetan Schizothoracinae fish provide a compelling example of adaptation to high-altitude environments. These fish have undergone genomic changes that facilitate survival in low oxygen and cold water conditions. The genetic basis of their adaptation includes genes involved in energy metabolism, transport, and immune response, reflecting the complex evolutionary processes that enable them to thrive in harsh aquatic environments (Tong et al., 2017).

Another example is the freshwater prawn genus *Macrobrachium*. Comparative transcriptomic studies on different species within this genus have identified genes associated with osmoregulation and stress response, which are crucial for adapting to varying salinity levels. These adaptations allow the prawns to maintain homeostasis and survive in diverse freshwater habitats (Rahi et al., 2019) (Figure 2).

The adaptation of fireflies to freshwater environments also provides insights into molecular mechanisms of adaptation. In the species *Aquatica leii*, significant genetic changes have been identified that enhance metabolic efficiency and morphological adaptations, enabling these fireflies to thrive in freshwater conditions (Zhang et al., 2020).

Figure 2 presents heatmaps showing the differential expression patterns of transcripts at 0‰ and 15‰ salinities for three different *Macrobrachium* species. (a) *M. australiense*: This heatmap shows the expression patterns of 876 transcripts under two salinity conditions. In the heatmap, red indicates upregulated expression, green indicates downregulated expression, and black indicates no significant change. Numbers 1, 2, and 3 represent three biological replicate samples. (b) *M. tolmerum*: This heatmap displays the expression changes of 861 transcripts at 0‰ and 15‰ salinities. Similar to (a), red and green represent upregulated and downregulated expression, respectively, while black indicates no significant change. The heatmap also includes three biological replicate samples. (c) *M. novaehollandia*e: This heatmap shows the expression patterns of 925 transcripts under different salinity conditions. Red indicates upregulation, green indicates downregulation, and black indicates no change, with three biological replicate samples labeled as 1, 2, and 3. By comparing the differential expression patterns of these three *Macrobrachium* species under varying salinity conditions, significant differences in transcript expression can be observed. Each species exhibits specific expression responses to different salinities, reflecting their varying adaptations to environmental salinity changes. These heatmaps provide crucial information for researchers to understand the gene expression regulatory mechanisms of different *Macrobrachium* species under salinity stress. Such differential expression analysis helps to identify key genes associated with salinity tolerance, thereby providing a theoretical basis for the conservation and aquaculture of these species (Adapted from Rahi et al., 2019)

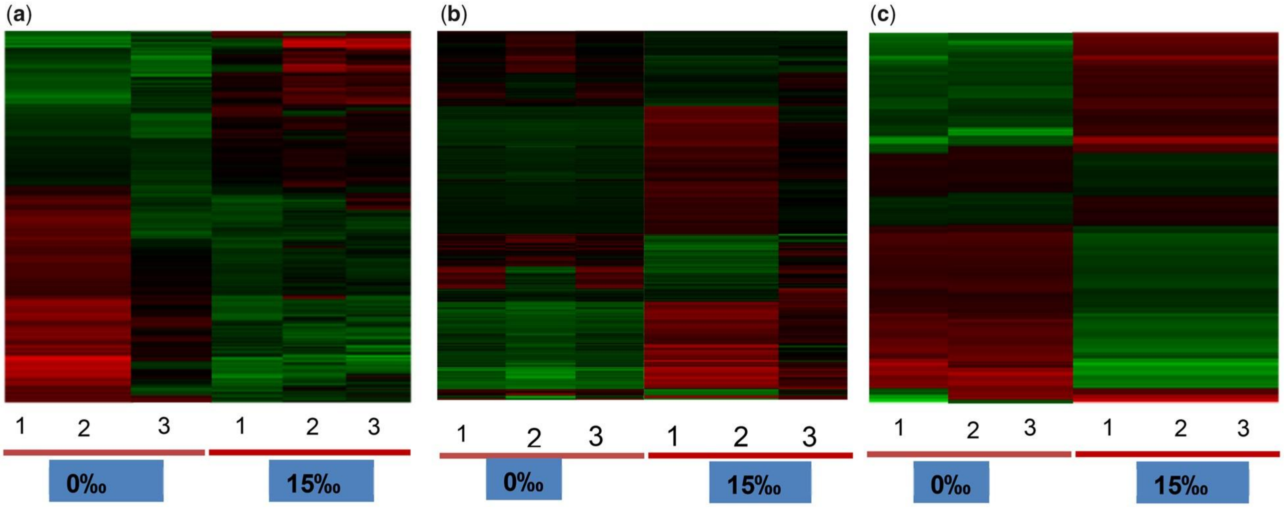

Figure 2 Heatmap showing differential expression pattern of transcripts at 0 & and 15 & salinities for three different *Macrobrachium* species (Adopted from Rahi et al., 2019)

Image caption: (a) *M. australiense* (876 transcripts), (b) *M. tolmerum* (861 transcripts), and (c) *M. novaehollandiae* (925 transcripts) (Adopted from Rahi et al., 2019)

6.3 Comparative analysis

Comparing adaptation mechanisms in marine and freshwater species reveals both commonalities and unique strategies. Both environments require species to develop efficient osmoregulation mechanisms to cope with salinity variations. For instance, both Gulf killifish and freshwater prawns exhibit genetic adaptations related to ion transport and osmoregulation, highlighting the convergent evolution of these traits in response to salinity challenges (Oziolor et al., 2019; Rahi et al., 2019).

However, differences arise in the specific environmental pressures and adaptive responses. Marine species often face greater challenges related to hypoxia and pressure, as seen in cetaceans, which have evolved unique genetic adaptations for efficient oxygen use and deep diving capabilities (Tsagkogeorga et al., 2015). In contrast, freshwater species like the Tibetan Schizothoracinae fish primarily adapt to temperature and oxygen fluctuations at high altitudes, with genetic changes focusing on energy metabolism and immune response (Tong et al., 2017).

Overall, the study of adaptation in aquatic species underscores the importance of both phenotypic plasticity and genetic evolution in enabling species to survive and thrive in diverse and changing environments.

Figure 3 illustrates the immune characteristics of *Schizothoracine* fish (*G. p. ganzihonensis*), including their innate immune system and Toll-like receptor (TLR) signaling pathway, as well as the mortality rates from two major infectious diseases. Panel (a) shows a schematic diagram of the innate immunity and the TLR signaling pathway in *Schizothoracine* fish. Four positively selected genes (PSGs) are highlighted in the TLR pathway: TLR3, IL10, IRF8, and TNFRSF1b. The innate immune response of these fish to pathogen invasion involves four major families: TLRs (Toll-like receptors), ILs (interleukins), IRFs (interferon regulatory factors), and TNFs (tumor necrosis factors). When a pathogen invades, genes from these families are activated to initiate an immune response to combat the infection. TLR stands for Toll-like receptor, IL stands for interleukin, IRF stands for interferon regulatory factor, and TNF stands for tumor necrosis factor. Panel (b) displays the mortality rates of

Schizothoracine fish due to two major infectious diseases: white spot disease and saprolegniasis. The bar graph indicates that the mortality rate for white spot disease is nearly 100%, whereas the mortality rate for saprolegniasis is also high but slightly lower than that of white spot disease. These results suggest that *Schizothoracine* fish have weak resistance to these pathogens, particularly white spot disease, which is almost fatal. Overall, this figure highlights the innate immune mechanisms of *Schizothoracine* fish and their response to pathogen invasion, while also revealing the high mortality rates when facing white spot disease and saprolegniasis. This information is crucial for understanding the immune characteristics of *Schizothoracine* fish and developing measures to control their infectious diseases (Adapted from Tong et al., 2017).

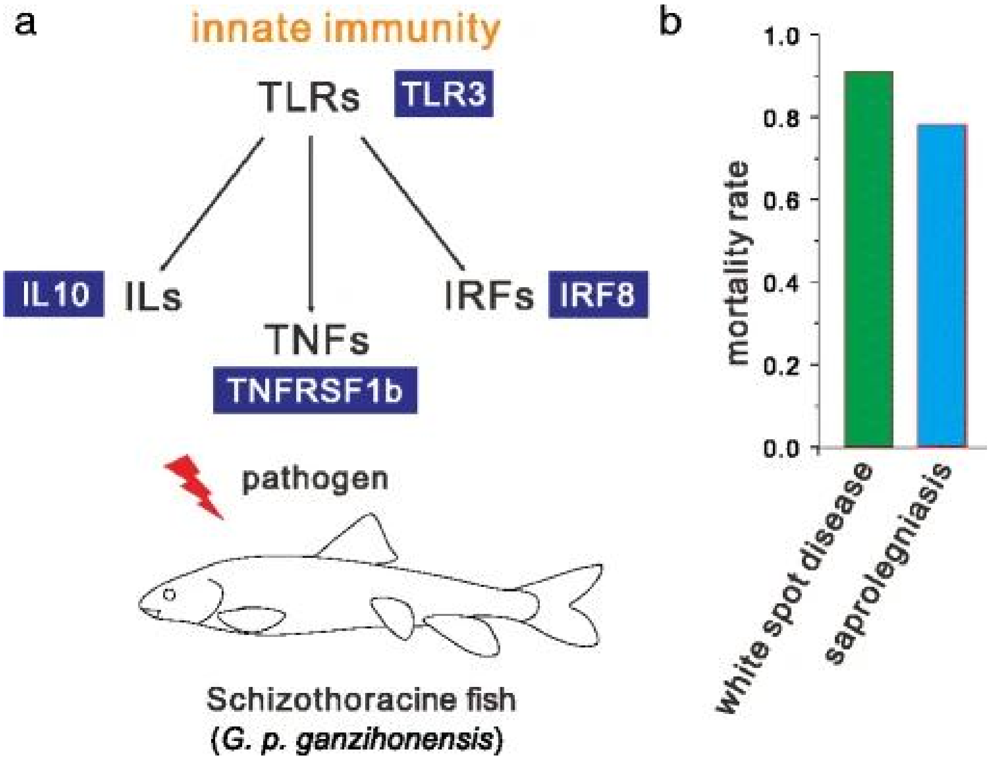

Figure 3 Immune characterizations of Schizothoracine fish (Adopted from Tong et al., 2017)

Image caption: a Schematic diagrams of innate immunity and Toll-like receptor (TLR) signing pathway. Four PSGs are highlighted in TLR pathway. The fish innate immune response to pathogens invasion, four major families are involved. TLR = toll-like receptor; IL = interleukin; IRF = interferon regulatory factor; TNF = tumor necrosis factor. b The morality rates of two culprit infectious diseases in Schizothoracine fish (Adopted from Tong et al., 2017)

7 Applications and Implications

7.1 Conservation and management

Understanding the mechanisms of adaptation in aquatic species has profound applications and implications for various fields, including conservation, aquaculture, fisheries management, and environmental science. This section discusses the importance of these applications and how they can help mitigate the impacts of environmental changes on aquatic ecosystems.

Adaptation mechanisms in aquatic species are crucial for informing conservation strategies and management practices. Knowledge of how species adapt to changing environments can guide efforts to preserve biodiversity and ecosystem services. For instance, conservation strategies can be tailored to protect habitats that support the adaptive capacities of species, such as breeding grounds and migratory routes.

The study of local adaptation is essential for effective conservation planning. For example, the research on Olympia oysters (*Ostrea lurida*) demonstrated local adaptation to low salinity events, which are expected to become more frequent with climate change. This information is critical for restoration efforts, as it suggests that sourcing oysters from populations adapted to similar environmental conditions can enhance the success of restoration projects (Bible and Sanford, 2016). Genomic tools can help identify populations that are genetically equipped to withstand environmental stressors. For instance, studies on redband trout (*Oncorhynchus mykiss gairdneri*) identified genomic regions associated with adaptation to thermal gradients. This knowledge can inform conservation actions by prioritizing the protection of genetic diversity critical for adaptation to future climate conditions (Andrews et al., 2022).

7.2 Aquaculture and fisheries

Aquaculture and fisheries can benefit significantly from understanding adaptation mechanisms in aquatic species. Selective breeding programs can utilize genetic information to enhance traits such as disease resistance, growth rates, and environmental tolerance, thereby improving the productivity and sustainability of aquaculture operations.

For example, transcriptomic studies on freshwater prawns (*Macrobrachium* species) revealed genes involved in osmoregulation and stress response, which are vital for adapting to different salinity levels. This information can be used to develop breeding programs that produce prawns with enhanced tolerance to varying salinity conditions, improving their survival and growth in diverse aquaculture settings (Rahi et al., 2019).

Fisheries management can also leverage adaptation knowledge to ensure the sustainability of fish stocks. Understanding how fish populations adapt to changing environmental conditions, such as temperature and salinity, can inform management practices that support the resilience of fish stocks. For instance, genomic studies on marine diatoms have shown rapid thermal adaptation, which can help predict how fish populations may respond to warming oceans and guide the development of adaptive management strategies (O'Donnell et al., 2018).

7.3 Predicting responses to environmental change

Predicting the responses of aquatic species to environmental changes is essential for mitigating the impacts of climate change and other anthropogenic stressors. Adaptive models that incorporate physiological limits, phenotypic plasticity, evolutionary adaptation, and dispersal can improve the accuracy of predictions and guide conservation and management actions.

A study using the AdaptR modeling approach demonstrated that accounting for adaptive capacity reduces projected range losses for Australian fruit flies by up to 33% by 2105. This approach can be applied to other species to predict their responses to environmental changes and identify critical areas for conservation efforts (Bush et al., 2016) (Figure 3).

Furthermore, research on aquatic insects and their adaptation to stream flow regimes provides insights into how species may respond to changing hydrological conditions. These findings can inform the design of river restoration projects that support the adaptive capacities of aquatic species, ensuring their long-term survival in altered flow regimes (Mazzucco et al., 2015).

Figure 4 shows the timeline of changes in the range size of three species of *Drosophila* under the CanESM2 climate change projections: (a) *Drosophila melanogaster* (continental distribution), (b) *D. simulans* (east coast), and (c) *D. rubida* (Wet Tropics). Each plot illustrates projections where CTmax (maximum heat tolerance) is held fixed (blue) and when plasticity and genetic adaptation are included (red). The data represent the mean and one standard deviation of 100 runs. (a) *Drosophila melanogaster*: Displays changes in distribution across the continental range. The blue line represents projections with fixed CTmax, while the red line represents projections including plasticity and genetic adaptation. (b) *D. simulans*: Shows changes in distribution along the east coast. Again, the blue and red lines represent fixed CTmax and adaptive projections, respectively. (c) *D. rubida*: Shows changes in distribution in the Wet Tropics region. The blue line indicates fixed CTmax projections, and the red line indicates projections with plasticity and genetic adaptation. (d) Shows the mean CTmax (°C) over time for each species in adaptive runs. The orange, green, and purple lines correspond to the species in panels (a), (b), and (c), respectively, displaying the mean CTmax and one standard deviation over time. Overall, Figure 3 illustrates how the distribution range and maximum heat tolerance of *Drosophila* species change over time under different climate change scenarios, particularly highlighting the differences between fixed CTmax and adaptive projections. These results help understand the potential impacts of climate change on species distributions and emphasize the importance of genetic adaptation in responding to climate change (Adapted from Bush et al., 2016).

8 Challenges and Future Directions

8.1 Methodological challenges

The study of adaptation in aquatic species presents numerous challenges and opportunities for future research. This section explores the methodological challenges, knowledge gaps, and emerging trends and innovations in the field. Researching adaptation in aquatic species involves several methodological challenges. One significant challenge is the difficulty of conducting long-term studies in natural settings, which are necessary to understand the full scope of adaptation processes. Additionally, the complexity of aquatic ecosystems, with their diverse biotic and abiotic interactions, makes it challenging to isolate specific factors driving adaptation.

High-throughput sequencing technologies have revolutionized our ability to study genetic adaptation, but they also present challenges related to data analysis and interpretation. The vast amount of data generated requires advanced computational tools and bioinformatics expertise to accurately identify adaptive genetic changes. Furthermore, the integration of genomic data with ecological and phenotypic data remains a complex task that requires multidisciplinary approaches (Wang and Guo, 2019).

8.2 Knowledge gaps and research opportunities

Several knowledge gaps exist in our understanding of adaptation mechanisms in aquatic species. One major gap is the limited understanding of the role of epigenetic modifications in adaptation. While studies have shown that epigenetic changes can facilitate rapid phenotypic responses to environmental changes, the long-term effects and heritability of these changes are not well understood (Niinemets et al., 2017).

Another knowledge gap is the insufficient understanding of the interaction between genetic and environmental factors in shaping adaptive responses. For instance, while we know that gene flow can influence local adaptation, the specific conditions under which gene flow facilitates or hinders adaptation are not fully understood (Calosi et al., 2016).

Research opportunities lie in studying the adaptive responses of lesser-known species and ecosystems. Most studies focus on well-known species with significant ecological or economic importance, but understanding adaptation in a broader range of species can provide more comprehensive insights into the mechanisms of adaptation (Miller et al., 2020).

8.3 Emerging trends and innovations

Emerging trends in the study of adaptation in aquatic species include the use of novel genomic and analytical techniques. The application of "resurrection genomics," which involves comparing historical and contemporary populations, allows researchers to directly observe genetic changes over time. This approach has provided valuable insights into the rapid adaptation of species such as Daphnia pulicaria to increased salinity in freshwater ecosystems (Wersebe and Weider, 2022).

The integration of evolutionary theory into conservation and management practices is another emerging trend. Understanding the adaptive potential of species can inform the development of conservation strategies that enhance the resilience of ecosystems to environmental changes. For example, adaptive models that incorporate evolutionary adaptation and phenotypic plasticity can help predict species' responses to climate change and guide conservation efforts (Bush et al., 2016).

Innovations in environmental DNA (eDNA) and metabarcoding techniques are also enhancing our ability to monitor and study aquatic biodiversity. These methods allow for the non-invasive sampling of genetic material from water, providing detailed information on species presence and genetic diversity. Such advancements can significantly improve our understanding of the adaptive responses of aquatic species to environmental changes (Corrales et al., 2019).

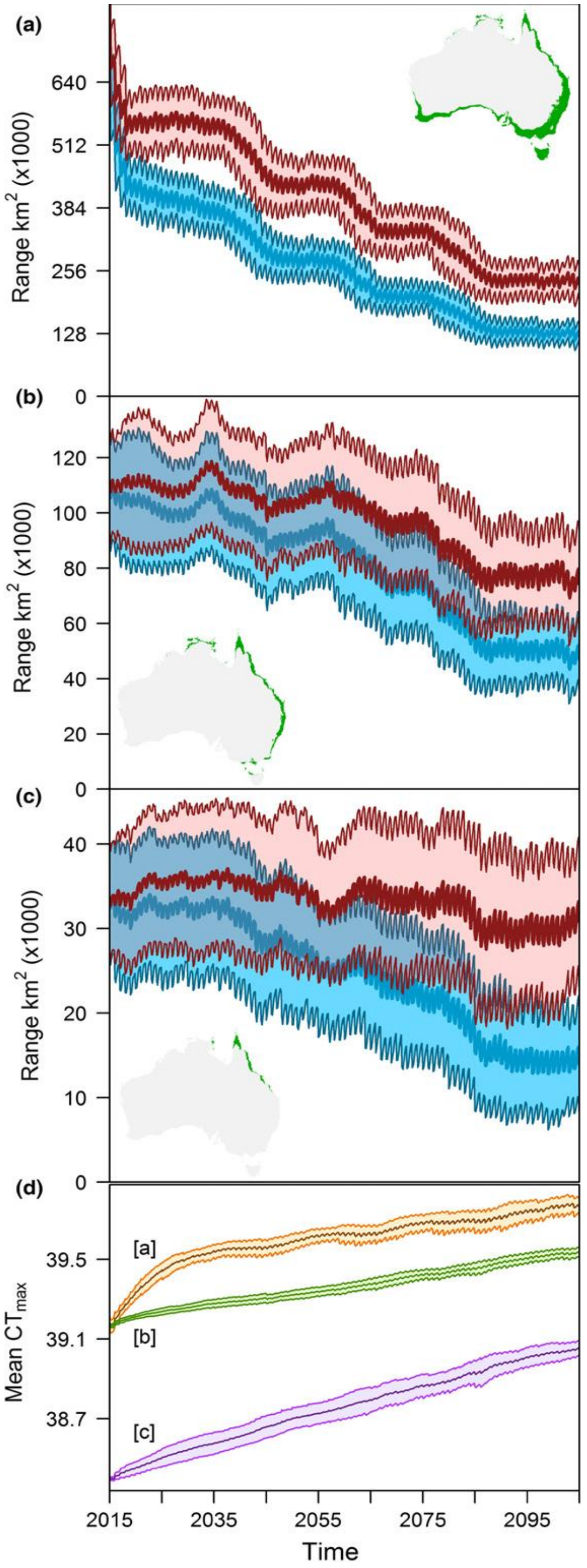

Figure 4 Timeline of changes in range size of (a) Drosophila melanogaster (continental distribution), (b) D. simulans (east coast) and (c) D. rubida (Wet Tropics) under the CanESM2 climate change projections (Adopted from Bush et al., 2016)

Image caption: Each plot shows timelines for projections in which CTmax is held fixed (blue), and when plasticity and genetic adaptation are included (red) (mean 1 SD of 100 runs). For runs with adaptation, panel (d) shows each species mean CTmax (1 SD) (°C); a – c, respectively, over time (Adopted from Bush et al., 2016)

9 Concluding Remarks

This research has explored various mechanisms of adaptation in aquatic species, focusing on phenotypic plasticity, genetic evolution, and molecular mechanisms. Aquatic species exhibit significant phenotypic plasticity, which allows them to respond rapidly to environmental changes. For instance, changes in gene expression related to osmoregulation and metabolic processes have been documented, demonstrating how species can adjust their physiology to cope with varying conditions.

Genetic evolution plays a crucial role in long-term adaptation, driven by processes such as mutation, natural selection, and genetic drift. Studies on marine mammals and freshwater prawns highlight the role of specific genes in adaptation to aquatic environments. Furthermore, molecular adaptations involve gene regulation, genomic changes, and epigenetic modifications, as seen in fireflies and marine diatoms, which provide insights into the genetic basis of adaptation to varying environmental conditions.

Integrative approaches that combine genomics, ecology, and evolutionary biology are crucial for understanding the full scope of adaptation in aquatic species. By integrating genomic and phenotypic data, scientists can identify specific traits that confer survival advantages under different environmental conditions. This comprehensive perspective enables better predictions of species' responses to climate change and other stressors, aiding in the development of effective conservation strategies.

Moreover, applying genomic insights to conservation practices can help maintain genetic diversity and adaptive potential in endangered species, ensuring their survival in changing environments. For example, the study of local adaptation in estuarine foundation species like the Olympia oyster has informed restoration efforts by emphasizing the importance of sourcing oysters from populations adapted to similar environmental conditions. Similarly, adaptive models that incorporate evolutionary adaptation and phenotypic plasticity can help predict species' responses to climate change and guide conservation efforts.

Future research should address several areas to advance our understanding of adaptation in aquatic species. First, more studies are needed to understand the role of epigenetic modifications in long-term adaptation and their heritability. Epigenetic changes, such as DNA methylation and histone modifications, play a significant role in regulating gene expression without altering the underlying DNA sequence, providing a rapid and reversible means of adaptation. Expanding research to include a broader range of species will provide more comprehensive insights into the mechanisms of adaptation and enhance our understanding of biodiversity. Many studies focus on well-known species with significant ecological or economic importance, but investigating lesser-known species can reveal new adaptive strategies and contribute to biodiversity conservation.

Developing advanced genomic tools and integrating ecological, genetic, and physiological data will improve our ability to identify adaptive genetic changes and understand their functional implications. High-throughput sequencing technologies have revolutionized our ability to study genetic adaptation, but they also present challenges related to data analysis and interpretation. Advanced computational tools and bioinformatics expertise are required to accurately identify adaptive genetic changes and integrate them with ecological and phenotypic data.

Conservation efforts should focus on preserving genetic diversity critical for adaptation to future environmental conditions. Genomic tools can help identify populations that are genetically equipped to withstand environmental stressors, guiding conservation actions to prioritize the protection of genetic diversity. This approach enhances the resilience of ecosystems to environmental changes and supports the long-term survival of species.

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Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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