

Physiological, Biochemical, and Molecular Responses of Himalayan Cold-Water Teleosts to Thermal and Hypoxic Stress: A Comprehensive Review

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ABSTRACT

Himalayan freshwater ecosystems support diverse and highly specialised cold-water teleosts, including snow trout (*Schizothorax* spp.) and golden mahseer (*Tor putitora*), which are adapted to cold, oxygen-rich, and highly dynamic mountain streams. However, climate change, increasing water temperatures, altered hydrological regimes, glacial retreat, and anthropogenic habitat modification are progressively exposing these stenothermal fishes to the interacting stresses of thermal warming and environmental hypoxia. This review synthesises current knowledge on the physiological, biochemical, molecular, behavioural, and immunological responses of Himalayan cold-water teleosts to these interacting stressors. Rising temperature simultaneously increases metabolic oxygen demand and reduces the oxygen-holding capacity of water, thereby constraining aerobic scope and imposing substantial cardiorespiratory limitations. Under severe oxygen limitation, fishes increasingly rely on anaerobic metabolism, resulting in lactate accumulation, metabolic depression, cellular acidification, and reduced energy allocation toward growth and reproduction. Respiratory and cardiovascular adjustments, including changes in gill morphology, ventilation, cardiac performance, and nitric oxide signalling, provide important compensatory mechanisms, although these responses become insufficient when thermal and oxygen thresholds are exceeded. At the molecular level, activation of the hypothalamic-pituitary-interrenal axis, hypoxia-inducible factor-1 α (HIF-1 α), heat shock proteins (HSP70 and HSP90), and associated stress-response pathways facilitates cellular acclimation. Concurrent mitochondrial dysfunction and reoxygenation can promote excessive reactive oxygen species generation, leading to oxidative damage and activation of antioxidant defences involving superoxide dismutase, catalase, and glutathione peroxidase. Prolonged stress further contributes to behavioural disruption, immunosuppression, increased disease susceptibility, and ecological vulnerability. The combined effects of warming and hypoxia therefore represent a critical physiological bottleneck for Himalayan cold-water fishes and may threaten their long-term persistence and ecosystem functions. Future research should emphasize integrated physiological, transcriptomic, metabolomic, and multi-omics approaches, together with field-based assessments of critical thermal and oxygen thresholds across altitudinal gradients. Incorporating these physiological indicators into conservation planning, environmental-flow management, and regulation of riverine development will be essential for safeguarding Himalayan cold-water fish biodiversity under ongoing climate change.

Keywords: Himalayan cold-water teleosts, thermal warming, environmental hypoxia, aerobic scope, physiological stress response

1. Introduction

Freshwater resources constitute a vital yet severely vulnerable component of the global biosphere, supporting immense biological diversity despite covering a minute fraction of the Earth's surface (Revenga et al., 2005; Dudgeon et al., 2006). Zooming into high-elevation environments, the Himalayan freshwater resources—comprising dynamic networks of snow-fed rivers, glacial meltwater streams, high-altitude lakes, and torrential springs—provide the primary hydrological lifeline for millions of downstream inhabitants while maintaining unique aquatic habitats (Vtorov et al., 2012; Raina & Petr, 1999). These torrential ecosystems harbor a remarkable spectrum of ichthyofaunal diversity characterized by high levels of endemism and specialized life-history traits adapted to extreme hydrodynamic conditions (Mir et al., 2013). Among this

assemblage, cold-water stenothermal fishes, most notably snow trouts (*Schizothorax* spp.) and the iconic golden mahseer (*Tor putitora*), represent the ecological keystones of these high-gradient mountain streams (Ali et al., 2021).

However, anthropogenic pressures compounded by accelerating global climate change are heavily destabilizing these fragile aquatic habitats (Sarkar et al., 2012). Rising global atmospheric temperatures translate directly into altered hydrological regimes, reduced winter snowpacks, and accelerated glacial retreat, culminating in severe thermal stress across Himalayan river basins (Ali et al., 2021). Crucially, this thermal loading acts in direct synergy with oxygen depletion: as water temperature increases, its capacity to hold dissolved oxygen declines precipitously, while the metabolic oxygen demand of resident aquatic organisms escalates exponentially, thereby precipitating environmental hypoxia (McBryan et al., 2013). At its core, thermal stress disrupts fundamental biochemical kinetics and enzymatic stability, while hypoxia impairs cellular respiration by restricting ATP production via oxidative phosphorylation (Lushchak, 2011; Wang et al., 2023). When experienced concurrently, these two environmental stressors impose profound physiological implications on fishes, ranging from the immediate collapse of aerobic scope and cardiorespiratory strain to systemic oxidative damage, endocrine exhaustion, and immunological suppression (Gamperl & Farrell, 2004; Abdel-Tawwab et al., 2019). While a detailed mechanistic breakdown of these metabolic, molecular, and biochemical bottlenecks forms the core of subsequent sections, understanding this overarching cascade is essential for evaluating the survival limits of indigenous Himalayan fish communities in a warming world.

2. Metabolic Scaling, Aerobic Scope, and Oxygen-Capacity Limitations

Stenothermal cold-water fishes evolved under stable, low-temperature, and oxygen-saturated hydrological regimes, endowing them with narrow thermal safety margins and high susceptibility to microclimate warming and localised pool hypoxia (Sharma & Langer, 2014). At the heart of environmental stress physiology is the Oxygen- and Capacity-Limited Thermal Tolerance (OCLTT) framework, which dictates that whole-organism thermal limits are set by the capacity of the cardiorespiratory system to supply sufficient oxygen to meet the exponentially rising metabolic demands of tissues (Pörtner & Farrell, 2008; Farrell, 2009). As ambient water temperatures rise, standard metabolic rate (*SMR*) increases continuously. Simultaneously, the physical solubility of oxygen in water declines, creating a physiological mismatch: metabolic oxygen demand escalates precisely when environmental oxygen availability shrinks (McBryan et al., 2013). This dual constraint dramatically compresses the factorial aerobic scope—the difference between maximum metabolic rate (*MMR*) and *SMR*—severely limiting the energy available for discretionary activities such as swimming against high-gradient torrents, foraging, and predator avoidance (Deutsch et al., 2020). In high-altitude and Himalayan cyprinids, such as the critically endangered snow trout *Schizothorax grahami* and the golden mahseer *Tor putitora*, chronic thermal stress coupled with restricted oxygen availability shifts energy partitioning away from growth and reproduction toward basal cellular maintenance (Bai et al., 2025; Kaur et al., 2025). When environmental oxygen tension falls below the critical oxygen partial pressure (P_{crit}), these stenotherms can no longer maintain aerobic homeostasis. Consequently, they are forced to prematurely upregulate anaerobic glycolysis to sustain ATP production. This metabolic shift triggers rapid lactic acid accumulation, cellular acidification, muscular fatigue, and systemic metabolic depression, forming the primary metabolic bottleneck for fish survival in warming, deoxygenated Himalayan riverine corridors (Basnayake et al., 2020).

3. Cardiorespiratory Adjustments and Gill Morphometric Plasticity

When facing the dual pressures of rising water temperatures and decreasing dissolved oxygen levels, high-altitude and hill-stream fishes rely heavily on immediate compensatory adjustments in their respiratory and cardiovascular systems. In the turbulent, high-gradient torrents typical of the Himalayas, maintaining adequate oxygen uptake requires structural and functional plasticity. Species such as the snow trout (*Schizothorax richardsonii*) exhibit specialised gill morphometrics, including modulated secondary lamellar surface area and inter-lamellar cell mass remodelling, which optimise diffusive oxygen transfer across water-blood barriers under fluctuating environmental conditions (Kumar et al., 2019; Singh & Sehgal, 2008). At the systemic level, cardiovascular performance is tightly regulated by adjustments in heart rate (*HR*), stroke volume, and cardiac output. The myocardial nitric oxide (NO) signalling pathway acts as a pivotal physiological bridge, modulating coronary vascular tone and protecting cardiac tissue against the damaging effects of hypoxic-reoxygenation cycles (Imbrogno et al., 2013; Filice et al., 2021). However, as thermal spikes intensify alongside severe hypoxia, myocardial oxygen requirements outstrip coronary supply. This mismatch precipitates cardiac arrhythmias, reduced stroke volume, and eventual systemic circulatory collapse, marking the upper thermal-oxygen boundary for stenothermal hill-stream teleosts (Gamperl & Farrell, 2004; Vornanen, 2016; Joshi et al., 2017; Tiwari et al., 2022).

4. Molecular Stress Axes and Gene Expression Networks

At the cellular and molecular levels, simultaneous thermal stress and hypoxia trigger rapid neuroendocrine cascades and extensive transcriptional reprogramming. The primary stress response involves the activation of the HPI axis, culminating in a surge of plasma cortisol and circulating catecholamines that mobilize metabolic substrates to sustain vital organ function under duress (Schreck & Tort, 2016). Concurrently, intracellular defence is orchestrated by conserved transcriptional regulators and molecular chaperones. Hypoxia-Inducible Factor (*HIF-1 α*) acts as the master transcriptional regulator of oxygen homeostasis, driving the upregulation of genes involved in anaerobic glycolysis, glucose transport, and erythropoiesis to compensate for low oxygen tension (Basnayake et al., 2020; Kumar et al., 2018). To mitigate the protein-denaturing effects of thermal spikes, chaperones such as Heat Shock Proteins (HSP70 and HSP90) are rapidly synthesised to refold damaged proteins and prevent cellular aggregation (Iwama et al., 2004). Transcriptomic profiling of high-altitude and Himalayan cyprinids confirms that these stress-response pathways are heavily modulated during environmental challenges, highlighting an evolutionary reliance on molecular adjustments to endure extreme habitat shifts (Zhang et al., 2020; Wang et al., 2023; Zhu et al., 2025).

5. Biochemical Alterations and Oxidative Stress Dynamics

The simultaneous disruption of mitochondrial electron transport chain efficiency during thermal and hypoxic stress accelerates electron leakage, leading to the excessive intracellular production of toxic Reactive Oxygen Species (ROS) (Livingstone, 2001; Lesser, 2006; Lushchak, 2011). In stenothermal and cold-adapted fishes, uncoupled mitochondrial respiration under thermal peaks combined with reoxygenation shocks triggers severe oxidative stress, marked by the overaccumulation of lipid peroxidation byproducts such as malondialdehyde (MDA) across hepatic, gill, and muscle tissues (Mustafa et al., 2020; Dar et al., 2022). To mitigate oxidative injury and protect cellular membrane integrity, cold-water cyprinids rely on an integrated enzymatic antioxidant defence network. This system is modulated primarily by Superoxide Dismutase (SOD), which dismutates superoxide radicals into hydrogen peroxide; Catalase (CAT); and Glutathione Peroxidase (GPx), which neutralise hydroperoxides (Menon et al., 2023; Dasgupta, 2026). However, chronic or acute fluctuations exceeding thermal-oxygen tolerance thresholds overwhelm these endogenous antioxidant reserves, culminating in cellular apoptosis, metabolic exhaustion, and tissue pathology (Mittal & Gupta, 2020).

6. Behavioural Profiles, Immunological Decline, and Disease Vulnerability

Physiological and biochemical exhaustion under thermal-hypoxic stress translates directly into disrupted behavioural profiles and severe ecological vulnerabilities. High-altitude and hill-stream fishes exposed to warming, deoxygenated waters exhibit classic behavioural avoidance strategies, such as increased surface respiration, localised migration toward cooler spring-fed tributaries, and a complete loss of stable rheotactic orientation in fast torrents (Sampaio & Freire, 2016; Bhatt & Pathak, 2021). Furthermore, prolonged activation of the neuroendocrine stress axis results in sustained high levels of circulating cortisol, which profoundly suppresses non-specific immune parameters—including lysozyme activity, total serum protein, and alternative complement pathway efficiency (Abdel-Tawwab et al., 2019). This physiological immunodepression compromises host disease resistance, rendering wild and cultured Himalayan fish stocks highly susceptible to secondary bacterial and parasitic infections, most notably virulent outbreaks of *Aeromonas salmonicida* (Sharma et al., 2021). Anthropogenic habitat fragmentation further exacerbates these compounding pressures by physically trapping fish populations in warming, stagnant riverine impoundments (Mir et al., 2013; Raina & Petr, 1999).

7. Conclusion

The synergy between rising water temperatures and environmental hypoxia acts as a severe, compounding physiological bottleneck for Himalayan cold-water teleosts, threatening biodiversity and ecosystem stability across high-altitude river basins. While specialized genera such as *Schizothorax* and *Tor* exhibit notable physiological, morphological, and molecular plasticity—ranging from gill remodeling and activation to antioxidant modulation—projected climate velocities far outpace natural evolutionary adaptation rates.

8. Knowledge Gaps

Significant knowledge gaps remain, particularly regarding the lack of high-throughput transcriptomic, metabolomic, and multi-omics data for many non-commercial, endemic hill-stream species inhabiting remote Himalayan watersheds.

9. Future Directions

Future research must prioritise empirical ecophysiological trials across broader altitudinal gradients to establish precise critical thermal maxima (CT_{max}) and critical oxygen thresholds (S_{crit}). Furthermore, these physiological insights must be directly integrated into regional conservation frameworks, ensuring science-based environmental flow (e-flow) allocations and strict ecological safeguards below hydropower installations to preserve the future of Himalayan riverine ecosystems.

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