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(Review Article)

A review on structure and functions of branchial gills in fishes

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Abstract

Fish gills represent one of the most functionally diverse and morphologically specialized organs among aquatic vertebrates, serving as the primary interface between internal physiology and the external aquatic environment. Beyond their classical role in respiration, gills perform multiple essential functions including ion and water regulation, acid–base balance, nitrogenous waste excretion, filter feeding, immune defense, and maintenance of overall homeostasis. These various physiological functions are supported by the structural complexity of the gills, which includes gill arches, gill rakers, filaments, and lamellae. Variations in gill morphology among species are strongly correlated with ecological niche, feeding strategies, and environmental conditions. Gill rakers, for instance, demonstrate remarkable adaptive diversity, ranging from elongated and densely packed structures in plankton feeders to short, spine-like projections in carnivores, reflecting the filtration and feeding mechanisms employed by the species . Similarly, the micro-anatomy of gill arches and filaments adapts to modulate water flow, optimize gas exchange efficiency, and reduce mechanical stress from the aquatic medium.

The gill is also a critical barrier organ whose epithelial surfaces form microbiological, chemical, physical, and immunological defense layers.

These surfaces are highly sensitive to fluctuations in temperature, salinity, ion concentration, pollution, and water quality. Environmental stressors, alongside dietary factors such as nutrient composition and feed formulation, strongly influence gill morphology and functional efficiency. Evidence indicates that nutritional modulation provides a more readily controllable strategy for enhancing gill integrity compared to environmental modification. This review synthesizes current scientific understanding of gill structure, function, and adaptive diversity, and critically evaluates the influence of feeding and environmental parameters on gill health. By integrating morphological, physiological, and ecological perspectives, the review underscores the significance of gill biology in fish growth, survival, and aquaculture productivity, providing a foundational framework for future research and sustainable fish health management.

Keywords: Fish Gills; Gill Morphology; Gill Physiology; Osmoregulation; Gas Exchange; Environmental Stressors; Nutritional Modulation; Aquaculture Productivity

1. Introduction

Fish gills represent one of the most physiologically complex and evolutionarily specialized organ systems among aquatic vertebrates (Evans & Nunez, 2015). As the primary interface between the internal milieu of the fish and the external aquatic environment, the gill is responsible for a suite of vital functions including respiration, osmoregulation, acid–base balance, nitrogenous waste excretion, immune defense, and feeding-related particle filtration (Evans & Nunez, 2015).Owing to this multiplicity of functions, even subtle structural variations in gill components can significantly influence the ecological fitness, feeding habits, physiological performance, and environmental adaptability of a species

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(Ou et al., 2013). Consequently, the study of gill morphology provides an indispensable framework for understanding the functional biology, ecological niche specialization, and adaptive evolution of teleost fishes (Almeida et al., 2013).

In teleosts, the gill apparatus is a highly vascularized structure composed of gill arches, rakers, filaments, and lamellae, each contributing uniquely to respiratory efficiency and feeding mechanisms. The delicate secondary lamellae facilitate counter-current gas exchange, while mitochondria-rich cells within the filaments maintain ionic and osmotic homeostasis. The morphological sophistication of these tissues reflects the ecological pressures exerted by variations in water temperature, oxygen availability, salinity, and flow regime. Numerous studies have demonstrated that gill structures are among the most environmentally sensitive tissues in fish, exhibiting rapid physiological and morphological plasticity in response to environmental fluctuations, pollutants, and dietary modifications. As such, gill morphology serves as both a bioindicator of environmental stress and a determinant of organismal health.

Among the structural components of the gill, the gill arches and gill rakers play additional crucial roles beyond respiration. Gill arches provide the mechanical scaffold for filaments and rakers, maintain the integrity of the buccopharyngeal cavity, and help modulate hydrodynamic pressure during ventilation. Their shape, curvature, and arrangement show significant interspecific variation, often correlating with habitat type and trophic ecology. Meanwhile, gill rakers—bony or cartilaginous projections on the branchial arches—act as selective filters during feeding. Their density, length, morphology, and spacing are closely associated with diet and feeding strategy. Planktivorous fish typically possess long, numerous, and closely spaced rakers specialized for fine particle filtering, whereas carnivorous species exhibit fewer, shorter, and more widely spaced rakers adapted for capturing larger prey. These variations make raker morphology an important taxonomic, ecological, and evolutionary marker.

Understanding such structural diversity becomes particularly relevant in freshwater ecosystems, where fish species inhabit dynamic and often challenging environments. Freshwater habitats commonly experience fluctuating dissolved oxygen, rapid changes in water chemistry, high organic load, and human-driven disturbances. These factors can influence gill architecture and function over both evolutionary and ecological timescales. Moreover, feeding ecology—and by extension, gill raker morphology—is profoundly shaped by the availability and type of prey organisms within these ecosystems. Studying gill morphology in freshwater species therefore offers insight into ecological adaptability, trophic dynamics, and environmental resilience.

Given this context, the present review paper undertakes a detailed examination of gill structure—particularly gill arches and gill rakers—in selected freshwater fishes. By analyzing morphological variations in relation to feeding habits, environmental conditions, and functional demands, the work aims to elucidate the adaptive significance of gill anatomy. This comparative approach not only enriches our understanding of teleost functional morphology but also provides critical information for fisheries biology, ecological assessment, species identification, and conservation management.

In summary, the gill constitutes one of the most informative anatomical systems in fish biology, bridging physiology, ecology, and evolutionary adaptation. A systematic investigation of gill architecture, supported by morphological measurements and species comparisons, is thus essential for comprehensively understanding the biology of freshwater fishes. This review paper seeks to contribute to this field by offering an integrative scientific interpretation of gill structural diversity and its ecological relevance.

2. Structural organization of fish gills

This section examines the anatomical diversity and adaptive significance of gill structures across teleost fishes. Fish gills are composed of four primary components—**gill arches, gill rakers, gill filaments, and secondary lamellae**—each intricately designed to optimize respiratory and feeding functions.

2.1. Gill Arches

Gill arches form the rigid skeletal framework that supports filaments and rakers. They vary widely among species in curvature, thickness, and segmentation, directly reflecting feeding ecology and environmental conditions.(Alsafy et al., 2013; Abumandour, 2016).

Comparative studies, such as in sea bream, sea bass, dusky grouper, European hake, puffer fish, and tilapia, reveal:

- Semilunar or crescentic shapes that reduce hydrodynamic resistance.
- Varying epibranchial–ceratobranchial ratios, which alter flexibility and mechanical stability.

- Interbranchial septa forming protective internal partitions.
- Presence of taste buds, which contribute to food selectivity.
- Species-specific modifications such as the suprabranchial dendritic organ of Clarias, adapted for air breathing.

Thus, the gill arch serves not only as a mechanical support but also as a key site for immune activity, sensory reception, and hydrodynamic pressure regulation (Drenner et al., 1987; Almeida et al., 2013).

2.2. Gill Rakers

Gill rakers are bony or cartilaginous projections on the anterior margin of the gill arch. Their number, size, spacing, and morphology closely correlate with feeding strategies:

- Planktivores possess long, slender, densely packed rakers forming fine filtration sieves.
- Herbivores exhibit moderately long rakers to trap plant debris.
- Carnivores show short, widely spaced, stout rakers often bearing sharp spines to prevent prey escape.

Examples provided in the review paper —from sea bass, sea bream, whitefish, Chaca chaca, and numerous freshwater species—demonstrate the role of rakers in both filtration-based feeding and prey retention.

Hydrodynamic studies indicate that gill rakers are not simply mechanical strainers but participate in cross-flow filtration, generating vortices that separate food particles from water (Van Wassenbergh et al. 2023).

2.3. Gill Filaments and Secondary Lamellae

Gill filaments (primary lamellae) house the microvascular respiratory surface. Secondary lamellae branch orthogonally to filaments, maximizing the exchange area. Microscopic observations in multiple species reveal:

- Pavement cells forming protective coverings with fingerprint-like microridges.
- Chloride cells enhanced with mitochondria for osmoregulation and ion transport
- Mucous cells that maintain epithelial hydration and create antimicrobial barriers.
- Structural variation in filament length, epithelial folding, and lamellar arrangement reflecting oxygen availability, flow regime, and osmotic conditions.

Together, these structures form the fundamental interface for respiration, ion regulation, and environmental sensing.

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3. Basic structure and ultrastructure of gills

This section synthesizes the morphological and ultrastructural features that constitute the teleost gill.

3.1. Morphological Structure

Teleost gills are arranged as paired holobranchs housed beneath the operculum. Each holobranch has:

- Gill arch (cartilaginous/bony support)
- Gill filaments (primary lamellae)
- Secondary lamellae for gas exchange
- Gill rakers for filtration
- Gill operculum for ventilation mechanics

The spatial arrangement—filament spacing, raker density, and lamellar distribution—determines respiratory efficiency, feeding selectivity, and mechanical protection of gill surfaces.

3.2. Ultrastructure

Scanning and transmission electron microscopy reveal three major epithelial cell types:

1. Pavement cells (≥90%) – carry microridges that stabilize mucus and enhance mechanical durability.
2. Chloride (mitochondria-rich) cells – specialize in active ion transport; regulate Na^+, Cl^-, and NH_4^+ fluxes.
3. Mucous cells – produce protective glycoproteins and antimicrobial agents.

These cells possess Golgi-dense cytoplasm, vesicular systems, and distinct microvilli, which contribute to secretory and absorptive functions.

3.3. Circulatory System

A precise vascular network maintains counter-current exchange:

- Afferent arteries → secondary lamellae capillaries → efferent arteries
- Ensures maximal O_2 uptake and CO_2 release
- Supports ammonia excretion and acid–base regulation

3.4. Neural Architecture

Innervation via cranial nerves VII, IX, and X coordinates:

- Ventilation movements
- Blood flow regulation
- Reflex responses to ionic or hypoxic stress

This demonstrates that gill function is intricately tied to nervous control for maintaining homeostasis. (Hanafy et al., 2020; Chen et al., 2014).

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4. Basic functions of fish gills

Fish gills perform multifunctional physiological roles indispensable to survival.

4.1. Gas Exchange

- Thin lamellar epithelium and counter-current flow maximize oxygen extraction.
- Large surface area facilitates diffusion of O_2 into blood and CO_2 out of blood.

4.2. Osmoregulation

- Chloride cells mediate active ion transport.
- Maintain internal ion balance in freshwater (ion-poor) vs marine (ion-rich) environments.

4.3. Acid–Base and Nitrogen Excretion

- Exchange of H^+, HCO_3^-, and NH_3 occurs across the gill epithelium.
- Gills serve as the primary organ for **ammonia excretion** in teleosts.

4.4. Feeding and Filtration

- Rakers filter particles, adaptively shaped to dietary niche.
- Turbulence and mucus allow efficient capture of plankton and detritus.

Respiratory, excretory, immunological, and nutritional functions are all integrated by the gill. (Nunez and Evans, 2015; Drenner et al., 1987).

5. Fish gill barrier function

This section outlines the four-tiered protective barrier formed by gill tissues.

5.1. Microbial Barrier

Gill surfaces harbour diverse microbiota, including Proteobacteria, Bacteroidetes, Actinobacteria, and Firmicutes. These:

- Compete with pathogens
- Assist in nitrogen cycling
- Are highly influenced by habitat and water quality

Species-specific communities reflect ecological niche and environmental stressors.

5.2. Chemical Barrier (Mucus and Antimicrobial Compounds)

Mucus contains:

- Mucins (glycoproteins for adhesion and viscosity)
- Immunoglobulins (IgM, IgT)
- Lysozyme, complement C3/C4
- Antimicrobial peptides (Hepcidin, LEAP-2, β-defensin)
- Antioxidant enzymes (CAT, GPX, SOD)

Oxidative stress markers such as **ROS, MDA, PC** indicate chemical barrier integrity.

5.3. Physical Barrier

Formed by:

- Tight junction proteins (Occludin, Claudins, ZO-1/ZO-2)
- Pavement cells with microridges
- Polarized epithelium

This barrier limits ion leakage, prevents metal entry, and maintains osmotic homeostasis.

5.4. Immune Barrier

Gill immune activity involves:

- GIALT (gill-associated lymphoid tissue)
- T lymphocytes, macrophages, leukocytes
- Cytokines (IL-1, IL-6, IL-8, TNF-α, TGF-β, IL-10 etc.)

These components regulate inflammation and pathogen defense.(Lowrey et al., 2015; Koppang et al., 2015; Chen et al., 2019).

6. Effects of feeding factors on gill barrier health

Gill health is strongly modulated by nutritional composition.

6.1. Proteins and Amino Acids

Appropriate protein levels:

- Upregulate TJ proteins (Occludin, Claudins, ZO family)
- Enhance antioxidant capacity (CAT, GPX, GST, GSH)

- Reduce oxidative markers (ROS, MDA, PC)
- Modulate immune gene expression and cytokine profiles
- Reduce gill inflammation

Functional amino acids such as **valine** and **arginine** improve ion regulation and mitigate metal-induced toxicity.

6.2. Lipids

Excess dietary lipids:

- Increase NF-κB p65 (pro-inflammatory)
- Suppress tight junction proteins
- Reduce antioxidant enzyme activity
- Lead to epithelial damage

6.3. Minerals

- **Iron overload** → gill erosion and oxidative stress
- **Phosphorus deficiency** → weakened immune function, increased apoptosis and oxidative damage
- Essential minerals maintain epithelial integrity and immunity.

6.4. Vitamins

6.4.1. Fat-soluble (E)

- Deficiency increases ROS, MDA, PC
- Weakens immune function and antioxidant systems
- Elevates apoptosis and inflammation

6.4.2. Water-soluble (Choline, Riboflavin, Folic acid, Pantothenic acid)

- Maintain immune enzyme activity (LA, ACP, complement)
- Regulate cytokines via NF-κB
- Protect antioxidant pathways
- Prevent apoptosis and epithelial deterioration

Proper vitamin balance is vital for optimal barrier integrity.(Chen et al., 2019; Cengiz et al., 2016).

7. Effects of environmental factors on gill health

Gill tissues are highly responsive to environmental disturbances.

7.1. Salinity

- Alters Na^+/K^+-ATPase activity and ionic transport
- Low salinity increases ion uptake; high salinity increases ion loss
- Extreme salinity causes irreversible gill tissue damage

7.2. pH

Low pH leads to:

- Lamellar fusion
- Excess mucus
- Edema and epithelial hyperplasia
- Impaired gas exchange

7.3. Temperature

Temperature shifts alter:

- Membrane lipid composition
- Na^+/K^+-ATPase activity
- Fatty acid saturation
- Cellular homeostasis

7.4. Nitrite

Nitrite causes:

- Methemoglobinemia
- Cytoplasmic damage
- Disruption of extracellular matrix synthesis
- Osmotic imbalance and K^+ efflux
- Production of toxic NO under low pH

7.5. Hypoxia & Ammonia

Hypoxia induces:

- Gill remodeling (lamellar extension)
- Apoptosis and mucous accumulation
- Reduced ionocyte area
- Upregulation of hypoxia-signaling genes (HIF family)

Ammonia impairs respiratory efficiency and epithelial transport.

7.6. Cyanides

Cyanide exposure disrupts **protein secondary structure**, compromising epithelial stability.

7.7. Pollutants and Nanoparticles

Nanoparticles (Ag, ZnO, Fe_2O_3, CNTs) cause:

- Mucus hypersecretion
- Gill edema and hyperplasia
- Inhibition of Na^+/K^+-ATPase
- Oxidative stress
- Immunosuppression

7.8. Heavy Metals

Metals (Cd, Cu, Pb, Ni, Fe):

- Accumulate in gills
- Cause structural damage
- Alter antioxidant enzyme profile
- Produce deformities, stunted growth, and impaired physiology
- Affect tight junction proteins and epithelial permeability

7.9. Effects on Aquatic Organisms

Chronic contaminant exposure leads to:

- Reduced growth, deformities, behavioural abnormalities.

- Bioaccumulation and biomagnification through the food chain.
- Declines in fish populations and ecosystem health (Bielmyer et al., 2012; Feng et al., 2015; Ou et al., 2013)

7.10. Research perspectives

This final section highlights the future directions for improving fish gill health:

- Water quality deterioration in aquaculture necessitates improved feeding strategies.
- Nutritional modulation (proteins, vitamins, minerals, amino acids) is an effective tool to **enhance gill barrier function**.
- Future research should optimize species-specific diets under variable environmental conditions.
- Integrating nutrient management with environmental monitoring will improve aquaculture sustainability, disease resistance, and growth performance (Chen et al., 2019; Evans & Nunez, 2015).

Compliance with ethical standards

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Disclosure of conflict of interest

There are no conflicts of interest between the authors and the publication of this article.

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