

Functional Significance of the Dual Respiratory System in Fishes: An Evolutionary and Physiological Perspective

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Abstract - Fishes are often introduced as archetypal water breathers, yet a substantial fraction of extant species routinely combine branchial gas exchange with air breathing through lungs, modified swim bladders, buccopharyngeal surfaces, gut epithelia, or accessory organs. This dual (bimodal) respiratory strategy is widely recognized, but its functional significance is still unevenly explained across evolutionary history, comparative physiology, and ecology. A key gap in the literature is the tendency to treat air breathing as a simple hypoxia response rather than as a multi-trait adaptive complex that restructures ventilatory control, cardiovascular function, ionoregulation, and life history. This review synthesizes evidence on why dual respiration evolved repeatedly, how it operates mechanistically, and what tradeoffs it imposes. Using a comparative, concept-driven review framework, I integrate studies on (i) selective pressures that favor aerial supplementation (environmental hypoxia, hypercapnia, temperature, drought, and episodic habitat instability), (ii) physiological partitioning of oxygen uptake and carbon dioxide excretion between gills and air breathing organs, (iii) cardiovascular and blood oxygen transport adjustments that enable effective bimodal exchange, and (iv) ecological consequences including niche expansion, resilience to climate-driven deoxygenation, and evolutionary stepping stones toward amphibious lifestyles. The central argument is that dual respiration is best understood as an evolutionary solution to variable oxygen landscapes that is maintained by conditional benefits and constrained by costs such as surface predation risk, energetic demands of ventilation, and tensions between gill reduction and ionoregulatory capacity. The review proposes a conceptual model linking environment, organ design, control systems, and performance outcomes, and identifies priorities for future research in a rapidly warming and deoxygenating world.

Keywords - air breathing fishes, bimodal respiration, hypoxia adaptation, gill remodeling, evolutionary physiology, oxygen transport, climate deoxygenation, accessory respiratory organs.

INTRODUCTION

The conventional framing of fish respiration begins and ends with the gill. This framing is pedagogically convenient but biologically incomplete. Across tropical floodplains, warm eutrophic lakes, seasonally drying wetlands, high-organic swamps, and even some relatively stable freshwater and marine habitats, fishes frequently supplement aquatic gas exchange with aerial respiration. The result is a dual respiratory system in which the gills remain important but are functionally partnered with an air breathing organ (ABO). This partnership is not rare. Air breathing has evolved many times independently within teleosts and is also present in several ancient lineages. The repeated emergence of bimodal breathing suggests that the selective pressures are common, that the physiological solutions are accessible, and that the resulting trait complex can be stable over evolutionary time.

Despite extensive descriptive work on air breathing organs and behavior, the field still faces a conceptual challenge: dual respiration is often reduced to a single driver (aquatic hypoxia) and a single outcome (survival). In reality, bimodal respiration

reorganizes multiple functional systems. It changes where and how oxygen is acquired, how carbon dioxide is eliminated, how acid-base balance is maintained, how circulation is regulated and partitioned, and how the animal navigates competing demands of feeding, predator avoidance, locomotion, and osmoregulation. These integrated changes mean that the functional significance of dual respiration extends beyond short-term hypoxia tolerance. It influences ecological niches, activity budgets, growth trajectories, reproductive strategies, and in some lineages the capacity for amphibious or semi-terrestrial living.

Problem statement

The core problem this review addresses is explanatory integration. Why do dual respiratory systems evolve repeatedly in fishes, and what physiological and evolutionary logic maintains them in the face of costs? A second, related problem concerns mechanistic generalization. Different fishes breathe air using different organs and different control strategies, yet broad comparative patterns exist. The review aims to clarify those patterns and propose an organizing model that links environment, morphology, control systems, and performance.

Existing debates and the research gap

Three debates recur in the literature. First, whether air breathing primarily evolves as a response to low dissolved oxygen or whether other drivers (temperature, CO₂, drought, toxic metabolites, competition) are equally important. Second, whether the adoption of air breathing is best described as a gain in capacity (adding an organ) or a reallocation problem (shifting gill design away from gas exchange toward ionoregulation). Third, whether dual respiration is a stepping stone toward terrestriality or mainly an aquatic persistence strategy in harsh habitats. These debates often proceed in parallel rather than being integrated. The research gap, therefore, is not a lack of observations but a lack of unified explanation that treats bimodal respiration as an adaptive complex with measurable tradeoffs.

Objectives and research questions

This review has four objectives: (1) to synthesize the evolutionary drivers of dual respiration across fish lineages, (2) to explain the physiological mechanisms that enable effective partitioning of gas exchange between gills and ABOs, (3) to evaluate the costs and constraints that shape the diversity of dual respiratory phenotypes, and (4) to propose a conceptual model that can guide empirical research under contemporary environmental change.

Research questions are: What environmental and ecological conditions repeatedly favor the evolution of dual respiration? How do fishes allocate oxygen uptake and carbon dioxide elimination between water and air? What cardiovascular and hematological adjustments support bimodality? What are the main tradeoffs and constraints, and how might they change under warming and deoxygenation?

II. LITERATURE REVIEW

Theoretical framework: adaptation in variable oxygen landscapes

Dual respiration can be framed within evolutionary physiology as a response to variability rather than extremes alone. In many habitats, dissolved oxygen is not simply low; it is unpredictable across diel cycles, seasons, and microhabitats. Adaptive responses to variability tend to favor traits that expand performance breadth and reduce risk of catastrophic failure. Bimodal respiration fits this logic: it adds a second exchange medium with different physical properties and constraints. Air contains far higher oxygen content than water, but accessing it requires surfacing and a set of morphological and control adaptations.

A second theoretical lens is tradeoff theory. Gills are multifunctional organs responsible not only for gas exchange but also ionoregulation, acid-base regulation, nitrogenous waste excretion, and in some contexts endocrine and immune functions. Increasing gill surface area tends to improve oxygen uptake but can raise ion loss in freshwater, water gain in seawater, and increase exposure to toxins and pathogens. The evolution of an ABO can relax the selection pressure to maximize gill respiratory capacity, enabling reduced gill surface area and thereby lowering osmoregulatory cost. This tradeoff between respiration and ionoregulation is central to modern understanding of why air breathing can be advantageous even when aquatic oxygen is not constantly low. A third lens is exaptation and organ co-option. The swim bladder and gut are not “designed” for respiration in most fishes, yet their tissues can be modified to support gas exchange under selection. The repeated emergence of air breathing suggests that multiple anatomical substrates can be recruited when selection favors it.

Major scholarly debates

Debate 1: Primary drivers. Hypoxia is clearly important, but in many systems hypoxia covaries with high temperature, high CO₂, high organic load, and seasonal drying. In some species, air breathing persists even when oxygen is not severely low, implying additional benefits such as enhanced aerobic scope, improved recovery from activity, or reduced gill-related ion costs.

Debate 2: Partitioning of O₂ and CO₂. Many bimodal breathers use air primarily for oxygen uptake while continuing to eliminate carbon dioxide mainly across the gills. This creates a functional asymmetry with important acid-base implications. The extent of this asymmetry varies across taxa and environmental contexts, and it shapes the evolution of ventilatory and circulatory control.

Debate 3: Terrestriality versus aquatic resilience. Some lineages (for example mudskippers and certain climbing fishes) show clear amphibious behaviors. Others use air breathing almost entirely as a coping strategy for poor water quality. Whether dual respiration tends to open terrestrial opportunities depends on correlated traits such as cutaneous permeability, locomotor capacity on land, and tolerance to desiccation.

Critical evaluation of prior work

A limitation of parts of the older literature is the dominance of organ description over integrative function. Conversely, some modern comparative physiology emphasizes general

mechanisms but can underplay lineage-specific history and ecological context. The most productive direction combines both: organ morphology must be read in relation to habitat oxygen regimes, gill design, blood properties, and behavior.

Conceptual model

I propose a four-layer model that treats bimodal respiration as an integrated system:

Layer 1 (environment): oxygen variability, temperature, CO₂, hydroperiod, and water chemistry.

Layer 2 (design): gill surface area and permeability, ABO surface area and vascularization, ventilatory structures.

Layer 3 (control): chemosensory control of ventilation, switching rules between water and air breathing, cardiovascular shunts and perfusion control.

Layer 4 (performance): aerobic scope, survival under hypoxia, osmoregulatory cost, growth and reproduction, ecological niche breadth.

This model structures the rest of the review and makes explicit that “dual respiration” is not a single trait but a coordinated phenotype.

ASCII schematic of the conceptual framework

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Environment (hypoxia, heat, CO2, drought, toxins)
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v
Design tradeoffs (gills <-> ABO capacity)
|
v
Control systems (ventilation switching, perfusion partitioning)
|
v
Performance outcomes (aerobic scope, osmoregulation, fitness, niche)
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III. METHODOLOGY

Theoretical approach

This article is a critical narrative review with a comparative evolutionary physiology orientation. It synthesizes evidence across lineages, habitats, and organ types to identify repeatable mechanisms and tradeoffs.

Analytical framework

The analysis follows the conceptual model above and organizes findings by (i) evolutionary drivers, (ii) organ diversity and functional design, (iii) physiological partitioning and control, and (iv) ecological and evolutionary consequences.

Source selection criteria

Sources are selected to meet three criteria: (1) peer-reviewed studies or major academic monographs in comparative physiology, fish biology, and evolutionary ecology; (2) explicit treatment of bimodal respiration or accessory respiratory organs, including quantitative measures of oxygen uptake partitioning, ventilatory control, or gill remodeling; and (3) representation of multiple taxonomic groups and organ types to support generalization. I prioritize studies that connect mechanism to ecological context.

Results or Thematic Analysis

Evolutionary origins: repeated solutions to recurring problems

Air breathing in fishes is a classic example of convergent evolution. The repeated origins indicate that the selective problem (variable aquatic oxygen and related stressors) recurs across habitats and that multiple anatomical routes can solve it. From an evolutionary perspective, the “dual respiratory system” emerges when (a) the marginal fitness benefits of accessing atmospheric oxygen exceed the costs of surfacing and maintaining an ABO, and (b) the necessary morphological substrate exists for modification (for example a vascularized swim bladder wall, buccopharyngeal epithelium, or gut tissue capable of increased diffusion capacity).

An important point is that air breathing does not always replace gill breathing. In many cases, it supplements gills in a context-dependent manner. This allows selection to favor flexible switching rules rather than obligate dependence, at least initially. Over time, some lineages become obligate air breathers, especially in habitats where water oxygen is predictably poor or where gills are reduced.

Environmental drivers: beyond “just hypoxia”

Hypoxia is the most direct driver because it limits aerobic metabolism. But several correlated drivers matter.

Temperature: Warm water holds less dissolved oxygen and increases metabolic demand. This combination compresses aerobic scope. In warm, stagnant waters, the advantage of breathing air is amplified because air oxygen availability is high while aquatic oxygen availability is low.

Hypercapnia and acid-base challenges: High CO₂ often accompanies hypoxia in dense vegetated waters and floodplains. If a fish relies solely on gills for CO₂ elimination in hypercapnic water, it may face acid-base stress. Some bimodal breathers retain gill CO₂ excretion but alter ion transport and buffering to manage acid-base balance. Others shift some CO₂ elimination to air breathing surfaces, though this is less common.

Seasonal drought and habitat instability: In temporary pools and wetlands, the risk is not just hypoxia but complete loss of water. Air breathing can extend survival and permit movement across short terrestrial distances, increasing persistence and dispersal.

Water chemistry and gill costs: In freshwater, large gill surface areas can increase ion loss. If a fish can acquire oxygen via air breathing, it can afford a smaller or less permeable gill, reducing ionoregulatory cost. This driver helps explain why air breathing may persist even when oxygen is not constantly low.

Diversity of air breathing organs and functional implications

Dual respiration is realized through diverse ABO designs. Four broad categories are common.

- True lungs and lung-like structures: Lungfishes represent an ancient, highly specialized solution. Lungs allow large aerial oxygen uptake, and in obligate air breathers they can sustain long periods when aquatic oxygen is inadequate.
- Modified swim bladders: In several lineages, the swim bladder becomes vascularized and functions as a respiratory organ. This solution leverages an existing gas-filled structure and can be highly effective for oxygen uptake.
- Suprabranchial and labyrinth organs: Anabantoids and some related groups possess specialized structures above the gills that trap air and provide large exchange surfaces. These organs often correlate with surface-oriented behaviors and allow exploitation of warm, stagnant waters.
- Buccopharyngeal and gut breathing: Some fishes use the lining of the mouth, pharynx, or intestine as an exchange surface. Intestinal breathing can be effective but often requires swallowing air, and it may impose constraints on feeding and digestion.

Functional implication: organ diversity changes the mechanics of ventilation (gulping, air retention, buccal pumping), the degree of reliance on air, and the tradeoffs with buoyancy control or feeding. For example, swim bladder breathing can interact with buoyancy, whereas gut breathing interacts with digestion and gut microbiome conditions.

Partitioning of gas exchange between water and air

A central functional feature of bimodal breathing is partitioning. In many species, air breathing provides a large fraction of oxygen uptake during hypoxia, while gills continue to dominate CO₂ excretion. This asymmetry is adaptive because CO₂ is far more soluble in water than oxygen and is often efficiently eliminated across gills even when oxygen uptake is constrained. However, reliance on gills for CO₂

excretion means the fish must maintain some gill perfusion and ventilation even when oxygen is primarily obtained from air.

Partitioning is dynamic, influenced by:

- ambient dissolved oxygen and temperature
- activity level and metabolic demand
- access to surface (vegetation cover, predation risk, current)
- developmental stage (juveniles may differ from adults)
- organ capacity (surface area, vascularization, diffusion distance)

A key insight is that partitioning is not only a response but also a driver of evolution. If air breathing increasingly supplies oxygen, selection can reduce gill respiratory capacity and thereby reduce water and ion flux across the gill surface. This can create a stable dual system where the gills are optimized more for ionoregulation and CO₂ excretion than for oxygen uptake. In extreme cases, the gills become so reduced that the fish becomes obligately air breathing for oxygen.

Control systems: switching rules and chemosensory regulation

Dual respiration requires decision-making by the organism, implemented through neural and chemical control systems. Switching between aquatic and aerial breathing is often regulated by:

- oxygen chemoreception: sensing low environmental oxygen and/or low arterial oxygen
- CO₂ and pH sensing: sensing acid-base disturbance
- mechanosensory cues and behavioral context: surface disturbance, predation cues
- internal state: stress hormones, activity demand, hunger

In many bimodal breathers, low water oxygen strongly increases air breathing frequency, but the exact threshold and response slope vary. These differences are functional: a lower threshold may confer safety in rapidly fluctuating oxygen environments but increases surface exposure costs. A higher threshold reduces risk and energy cost but may increase vulnerability during sudden hypoxic events. Thus, ventilatory control is a key site where ecological pressures and physiological constraints meet.

Cardiovascular integration: perfusion partitioning and oxygen transport

Dual respiration is not only about ventilation. It also requires delivering oxygen from the ABO to tissues efficiently. This often involves adjustments in:

- cardiac output allocation between gills and ABO
- vascular shunts that can bypass gills when water oxygen is low
- control of perfusion to the ABO during air breathing bouts

- hemoglobin properties (oxygen affinity, Bohr and Root effects)
- blood buffering and CO₂ transport

A general pattern in effective bimodal breathers is the capacity to increase ABO perfusion during air breathing while maintaining sufficient gill perfusion for CO₂ elimination and ionic regulation. Some species show functional separation of circulatory pathways that improves efficiency. Others rely on flexible modulation of vascular resistance.

Hemoglobin properties are also central. In hypoxic or warm environments, shifts in oxygen affinity can help maintain oxygen loading at the exchange surface and unloading at tissues. However, high affinity can reduce unloading, so the balance is context dependent. Many fishes also rely on strong pH sensitivity (Bohr effect) to tune oxygen delivery under varying acid-base conditions.

Ecological consequences: niche expansion and resilience

The functional significance of dual respiration becomes clearest when viewed ecologically.

Habitat expansion: Air breathing allows fishes to inhabit waters that would otherwise exclude aerobic species, such as hypoxic swamps, shallow floodplains, and warm stagnant ponds. It can also allow exploitation of microhabitats within otherwise oxygenated systems (dense vegetation, bottom layers).

Activity and foraging: In hypoxic waters, purely water-breathing fishes often reduce activity. Bimodal breathers can maintain higher activity because air breathing supplies oxygen, enabling continued foraging and predator avoidance.

Survival and persistence during extremes: In seasonal drought or nocturnal hypoxia, air breathing can be the difference between survival and mortality. This directly affects population persistence in variable climates.

Stepping stones toward amphibiousness: In some lineages, frequent surfacing and the ability to tolerate air exposure can facilitate brief terrestrial excursions. While not equivalent to true terrestriality, it can enable movement between pools or exploitation of shoreline resources.

Costs and constraints: why not all fishes are bimodal breathers

If air breathing is so useful, why is it not universal? The answer lies in costs, constraints, and ecological tradeoffs.

Surface predation risk: Surfacing can expose fishes to birds and other predators. In open water, this cost can be severe.

Energetic costs and time costs: Air breathing requires behavioral investment (surfacing, gulping, retaining air) and may conflict with feeding or avoiding predators.

Morphological constraints: Not all fishes have anatomical substrates that can be readily modified into efficient ABOs without compromising other functions (buoyancy, feeding).

Tradeoffs with gill functions: Reducing gill surface area can lower osmoregulatory cost, but it can also reduce capacity for ammonia excretion and acid-base regulation, particularly under certain environmental loads.

Physiological limits under extreme conditions: In very high CO₂ waters, maintaining acid-base balance can be difficult even with air breathing, especially if CO₂ elimination remains mainly branchial.

Discussion

Interpreting the functional significance: dual respiration as an adaptive complex

The central interpretive claim of this review is that dual respiration is not simply a backup system for oxygen scarcity. It is an adaptive complex that reorganizes multiple functions. The ABO increases access to oxygen, but the full advantage often emerges through secondary effects: the relaxation of selection on gill respiratory surface area, the reduction of ionoregulatory costs, and the expansion of ecological opportunity in variable habitats.

This interpretation helps reconcile apparent contradictions in the literature. Some fishes air breathe in moderately oxygenated water, which seems inconsistent with a simple hypoxia trigger model. Under the adaptive complex view, this is expected. If air breathing enables smaller gills, improves energy budgets under osmoregulatory stress, or increases aerobic scope during activity, it can be beneficial even when oxygen is not critically low.

Linking findings to theory: tradeoffs, plasticity, and repeated evolution

Tradeoff theory provides a strong explanation for repeated evolution. The gill is both a respiratory organ and a site of exchange with the external environment that can be physiologically costly. In freshwater, high gill permeability increases ion loss. In polluted or pathogen-rich waters, high gill exposure can increase risk. By shifting oxygen uptake to air, fishes can adopt gill designs better suited to these constraints. This creates a coherent selection gradient that can favor dual respiration in a wide range of habitats.

Plasticity is also important. Many air breathing fishes exhibit reversible gill remodeling in response to oxygen availability, changing lamellar exposure and epithelial thickness. Such plasticity provides immediate functional benefit and may facilitate evolutionary change by allowing individuals to survive in variable environments while selection acts on regulatory and structural traits.

Comparison with existing studies: toward integrated explanations

Across studies, there is strong agreement that hypoxia triggers air breathing behavior and that many air breathers show morphological and physiological adaptations. The added value of the present synthesis is to treat these observations as parts of a linked system: environment drives a switching rule; switching changes partitioning; partitioning reshapes selection on gills and blood traits; these in turn alter performance and ecology. This systems view is especially important for comparing distantly related lineages with different ABO designs, because it shifts attention from organ identity to functional roles and tradeoffs.

Broader implications: climate change, deoxygenation, and fish persistence

Fresh waters and coastal systems are experiencing warming, eutrophication, and episodic hypoxia in many regions. Under such trends, dual respiration may become more important as a resilience trait. However, the presence of an ABO does not guarantee resilience, because costs (surface exposure, habitat fragmentation) may also increase, and the benefits of air access depend on surface availability and behavioral safety. A key implication is that conservation and management should treat surface access and habitat structure as functionally relevant for air breathing fishes, especially in heavily vegetated, polluted, or human-modified waters where surface films, toxins, or barriers may constrain gulping.

IV. CONCLUSION

Dual respiratory systems in fishes represent one of the most striking examples of functional innovation under environmental variability. From an evolutionary perspective, their repeated emergence reflects recurring selection pressures in oxygen-variable habitats and the accessibility of multiple anatomical substrates for gas exchange. From a physiological perspective, bimodal respiration is sustained by coordinated changes in organ design, ventilatory and cardiovascular control, oxygen transport, and behavioral decision-making. The

functional significance extends beyond hypoxia survival: dual respiration can reduce osmoregulatory costs through altered gill design, maintain aerobic performance under warm and stagnant conditions, expand ecological niches, and in some lineages facilitate amphibious behaviors. At the same time, dual respiration is constrained by costs, including predation risk at the surface, energetic and time demands of surfacing, and tradeoffs with gill-based excretion and regulation. The review contributes an integrated conceptual framework that links environment, design, control, and performance, and it emphasizes that understanding bimodal respiration requires treating it as an adaptive complex rather than a single trait.

Policy or practical implications

In applied contexts, recognizing dual respiration as a resilience mechanism suggests that management of hypoxia-prone systems should consider not only dissolved oxygen levels but also surface access, habitat connectivity during drought, and water quality features that affect gulping and ABO function. In aquaculture and conservation, species-specific reliance on air breathing should inform handling practices and habitat design.

Limitations

As a synthesis, this article cannot provide exhaustive coverage of all air breathing lineages or all regional ecological contexts. Some mechanistic areas, particularly molecular regulation of gill remodeling and chemosensory control diversity across taxa, remain unevenly characterized. Future empirical work is needed to test causal links in the conceptual model, especially under realistic multi-stressor environments.

Future Research Directions

Several research priorities follow from this synthesis. First, comparative studies that quantify partitioning of oxygen and carbon dioxide exchange across multiple taxa under standardized multi-stressor conditions (oxygen, temperature, CO₂) would allow stronger generalization. Second, integrative experiments that couple gill remodeling, ionoregulation, and ABO use would clarify when reduced gill respiratory capacity is a benefit versus a liability.

Third, mechanistic work on neural and endocrine control of switching rules, including how predation risk and social context modulate air breathing, would connect physiology to ecology more tightly.

Fourth, phylogenetically informed analyses linking ABO design to habitat oxygen variability metrics would test the central hypothesis that variability, not only low mean oxygen, predicts bimodality.

Fifth, climate-relevant studies should examine how warming, deoxygenation, and pollution interact to reshape the cost-benefit balance of air breathing and to influence population persistence.

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