pH stress in bivalves: Effects on growth, calcification, and metabolic processes

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Received: March 2025 Accepted: June 2025

Abstract

Bivalves, which are vital to aquatic ecosystems and aquaculture, are highly susceptible to pH fluctuations caused by ocean and freshwater acidification. This review summarizes the physiological responses of various bivalve species to changes in pH, including effects on growth, shell calcification, metabolism, respiration, feeding, and excretion. Ocean acidification reduces the availability of carbonate ions, which inhibits shell formation and growth and can divert energy toward pH regulation. Species sensitivity varies: marine bivalves are particularly vulnerable to slight decreases in pH, whereas many freshwater species exhibit greater resilience due to their adaptation to variable habitats. Acidic conditions can induce metabolic depression to conserve energy or increase energy demands for maintaining homeostasis, resulting in reduced growth, higher mortality, and impaired reproduction. Feeding rates are highly sensitive to pH, with most bivalves showing optimal activity within a narrow pH range and reduced feeding under acidic stress. Understanding species-specific vulnerabilities and pH tolerance mechanisms is crucial for effective conservation in an increasingly acidified environment.

Keywords: Ocean acidification, bivalve physiology, calcification, pH tolerance, metabolic adaptation

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[DOI: 10.22034/INJBIR.3.2.151]

Introduction

Bivales are stationary and feed by filtering water; they remain in constant contact with their aquatic environment. This makes them highly sensitive to changes in their surroundings, particularly variations in pH levels (Gazeau *et al*., 2013). This sensitivity, combined with their roles as primary consumers, positions bivalves as key indicators of the impacts of acidification on aquatic systems (Kroeker *et al*., 2013; Parker *et al*., 2019).

As CO_2 reacts with seawater, it lowers the ocean's pH, reduces carbonate ion concentrations, and inhibits shell formation in calcifying organisms such as bivalves (Gattuso *et al*., 2018). This reduction in carbonate availability impairs calcification and shell integrity (Parker *et al*., 2013). For example, a pH decrease of just 0.2 units has been shown to reduce calcification by 25% in *Mytilus edulis* and by 10% in *Crassostrea gigas*, highlighting the sensitivity of bivalves to even minor pH changes (Gazeau *et al*., 2010; Thomsen *et al*., 2015).

Bivalve species exhibit varying pH tolerances due to their diverse adaptations to aquatic environments. Understanding these tolerance ranges is crucial for predicting responses to ocean and freshwater acidification and for informing conservation efforts and water quality criteria in bivalve aquaculture. Marine bivalves exhibit optimal growth in seawater with a pH range of 7.8 to 8.3, which is ideal for calcification, acid-base balance, and shell formation (Thomsen and Melzner, 2010). Even slight deviations from this pH range can induce stress, particularly in vulnerable larvae and juveniles (Griffith and Gobler, 2017). Freshwater bivalves typically tolerate a pH range of 6.5 to 9.0, which reflects the fluctuating pH levels of inland waters (Seitz *et al*., 2023; Wang *et al*., 2008). Species-specific tolerance varies considerably. Marine bivalves are generally more sensitive than freshwater species, with some tropical species exhibiting stress at pH 8.5, likely due to the historically narrower pH range in marine environments (Vlaminck *et al*., 2022). Blue mussels (*M. edulis*) tolerate pH levels ranging from 7.2 to 9.0, whereas Pacific oysters (*C. gigas*) thrive at pH levels between 7.5 and 8.2 but experience high mortality below pH 7.0 (Thomsen *et al*., 2015). Some deep-sea bivalves near hydrothermal vents exhibit remarkable tolerance, surviving in pH levels as low as 6.0 to 6.5 (Thomsen and Melzner, 2010). Zebra mussels (*Dreissena polymorpha*) tolerate pH levels from 6.0 to 9.5, but reproduce and grow best between 7.0 and 8.5 (Burlakova *et al*., 2014).

Low pH stress reduces bivalve growth and metabolism, leading to increased mortality. Juvenile sunray surf clams (*Mactra chinensis*) exhibit optimal growth at pH levels between 7.8 and 8.4; however, survival rates decline significantly outside this range. Notably, no clams survived after 24 hours at pH 9.6. Growth is optimal at pH 8.0, with significant reductions observed beyond this range, underscoring their sensitivity to pH fluctuations. Additionally, low pH induces oxidative stress by inhibiting antioxidant enzymes, reducing metabolic efficiency, and increasing vulnerability to cellular damage, ultimately threatening population survival (Istomina *et al*., 2021; Dai *et al*., 2023).

[DOI: 10.22034/INJBIR.3.2.151]

Most bivalves tolerate pH levels up to 9.0–9.5, beyond which physiological stress occurs. Above pH 9.0, maintaining acid-base balance becomes challenging because hydroxide ions interfere with ion transport (Gutowska *et al*., 2010). Elevated pH also alters mineral solubility, potentially causing irregular shell formation due to calcium carbonate precipitation without organic regulation (Ries, 2011). Bivalve tolerance to pH changes correlates with the environmental variability of their habitats. Species from dynamic estuarine and upwelling zones (e.g., *Mytilus chilensis*, *Argopecten purpuratus*) exhibit greater resilience to acidification than those from stable environments, suggesting that tolerance to pH fluctuations is an evolved trait in species exposed to variable conditions (Vialova, 2023).

Lower pH levels threaten bivalve survival. Bivalves experience physiological stress at pH levels below 7.6 to 7.8, with severe effects occurring below pH 7.4 (Kroeker *et al*., 2013). Calcification is notably inhibited below pH 7.7, where aragonite saturation becomes critically low for most species (Doney *et al*., 2020). Freshwater bivalves can tolerate low pH levels (4.5–5.0); however, chronic exposure to such acidic conditions reduces growth and reproduction and increases mortality (Heming *et al*., 1988; Dai *et al*., 2023). This tolerance likely arises from adaptations to naturally acidic freshwater environments and the presence of buffering compounds within these systems.

Environmental stressors increase the negative impacts of pH on bivalve physiology. For example, elevated CO_2 levels and increased temperatures synergistically increase mortality in *Saccostrea glomerata* larvae (Parker *et al*., 2010). Similarly, combined stressors reduce survival rates and shell thickness in *Argopecten irradians* and *Mercenaria mercenaria* (Talmage and Gobler, 2010). Larval stages are highly susceptible to pH fluctuations, which can cause reduced growth, delayed development, and increased mortality.

Understanding the physiological responses of species to pH changes is crucial for predicting ecosystem impacts. Given the ongoing decline in global pH levels and the economic significance of bivalve aquaculture (>$16.8 billion annually) (FAO, 2024), studying the effects of pH across diverse bivalve species remains a critical area of environmental physiology. This study examined growth, calcification, metabolism, respiration, feeding, and excretion in various marine, freshwater, and estuarine bivalve species. This integrative approach provides a comprehensive perspective on the effects of pH stress, revealing patterns of vulnerability and resilience that are often obscured in single-species or single-trait studies. The study highlights that species, particularly at various life stages (larvae, juveniles, adults), respond differently to environmental changes. The review examines findings on physiological responses—including growth, shell calcification, metabolism, respiration, feeding, and excretion—to provide a comprehensive understanding of how bivalves cope with pH stress.

Effect of pH on bivalve growth

Ocean acidification, caused by increased CO_2 levels and resulting in lower pH, reduces the availability of carbonate ions essential for shell formation in bivalves. This leads to slower growth, thinner shells, and higher mortality rates, particularly among young oysters, clams, and scallops (Talmage and Gobler, 2010; Waldbusser *et al*., 2015). Ocean acidification decreases the saturation of calcite and aragonite, the primary components of bivalve shells, thereby increasing the energy required for shell formation (Zhou *et al*., 2024). As a result, bivalves allocate energy away from growth and reproduction to maintain internal pH balance under acidic conditions (Liu *et al*., 2025). Juvenile sunray surf clams (*M. chinensis*) exhibit optimal growth at a pH of 8.0, with significant declines in growth observed outside the pH range of 7.8 to 8.4 (Dai *et al*., 2023). Acidification particularly harms smaller individuals and certain species, and its detrimental effects on growth and survival are intensified by stressors such as hypoxia and temperature fluctuations (Stevens and Gobler, 2018). Ocean acidification harms bivalve larvae. Larvae grown under preindustrial CO_2 conditions (characterized by higher pH) exhibit improved growth, survival, and shell formation compared to those exposed to current and future conditions (characterized by lower pH and increased acidity) (Talmage and Gobler, 2010; Liu *et al*., 2025). For example, research indicates that ocean acidification negatively impacts *C. gigas* growth. Specifically, juvenile oysters exposed to pH 7.6 exhibited a 25% reduction in shell growth compared to those at pH 8.1 (Gazeau *et al*., 2007). Atlantic bay scallop larvae (*A. irradians*) are more sensitive to ocean acidification than hard clams (*M. mercenaria*). The results indicated that low pH impairs growth and settlement in *A. irradians*, whereas blue mussel (*M. edulis*) and Atlantic surfclam (*Spisula solidissima*) show minimal responses, suggesting differing adaptive capacities among these species (Kroeker *et al*., 2010; Talmage and Gobler, 2010). Acidification decreases oyster larval development by disrupting the protein synthesis essential for shell formation. Low pH conditions reduce protein deposition efficiency by 30–40%, delaying calcification and resulting in shells that are 4–6% smaller than normal (Ledezma, 2024). Ocean acidification likely contributes to the decline of bivalves, as evidenced by deformed and eroded shells observed in acidic environments (Gattuso *et al*., 2018).

Further research is essential to understand bivalve adaptation and their evolutionary potential in response to these ongoing changes in ocean chemistry. Understanding species-specific vulnerabilities and developing adaptive management strategies are crucial for sustaining bivalve populations in an increasingly acidified ocean environment.

Shell formation and calcification processes

Shell formation and calcification are among the most extensively studied physiological responses to changes in pH. Bivalve shell formation requires an adequate supply of carbonate ions for calcium carbonate precipitation. A decrease in pH reduces the saturation levels of aragonite and calcite, thereby inhibiting calcification (Kroeker *et al*., 2013). Acidification impairs

[DOI: 10.22034/INJBIR.3.2.151]

calcification by directly dissolving secreted $CaCO_3$ and by suppressing the metabolic ion transport that maintains the chemistry of the calcifying fluid. In eastern oysters (*Crassostrea virginica*), pH levels below 7.6 cause shell dissolution rates to exceed 5 µm per day, forcing the oysters to expend energy on repair rather than growth (Ledezma, 2024). In another study, In *Mytilus galloprovincialis*, exposure to pH 7.4 during the trochophore stage (24–40 hours post-fertilization) reduced normal development to 56–64%, compared to ≥95% at pH 8.1. Low pH exposure, particularly during shell field formation and the transition from PDI (prodissoconch I) to PDII, caused abnormalities such as protruding mantles and malformed hinges. Diurnal pH cycles (7.8±0.4) reduced deformities compared to sustained low pH, suggesting that intermittent recovery periods can reduce the negative impacts of acidification (Kapsenberg *et al*., 2018). Ocean acidification threatens bivalves by causing shell deformities and developmental problems, which can lead to population declines that negatively affect marine ecosystems and aquaculture.

Metabolic and energetic costs of different level of pH

Reduced pH affects bivalve metabolic rates in complex ways, varying significantly depending on species, exposure duration, and pH level. Bivalve metabolic responses to reduced pH vary widely, ranging from metabolic depression to increased energy demand, depending on acidification and species-specific tolerances.

Bivalves often employ metabolic depression to survive under reduced pH conditions. For instance, Zhao *et al*. (2017) observed that blood clams (*Tegillarca granosa*) exposed to pH levels of 7.8, 7.6, and 7.4 over a 40-day period exhibited a significant reduction in respiration rates with the decrease in pH. Since respiration rate reflects metabolic energy expenditure, these findings suggest suppressed aerobic metabolism and reduced energy consumption under ocean acidification. This observation aligns with the broader understanding that metabolic depression is a common stress-response strategy among marine invertebrates (Guppy, 2004). Conversely, Shang *et al*. (2023) found that exposing thick-shelled mussels (*Mytilus coruscus*) to a pH of 7.7 for 14 days increased their metabolic activity. Elevated electron transport system activity indicated enhanced mitochondrial metabolism and a higher demand for ATP synthesis. This acidification exposure increased energy requirements but decreased cellular energy allocation, suggesting a greater metabolic cost to maintain homeostasis. In addition, In *M. coruscus*, osteoarthritis significantly alters the biosynthesis of phenylalanine, tyrosine, and tryptophan, as well as the metabolism of taurine, hypotaurine, glycine, serine, and threonine. These changes in amino acid metabolism likely reflect the energy required to maintain acid-base balance and potential compensatory responses (Shang *et al*., 2023). Vialova (2023) found that the commercially important species *M. galloprovincialis* and *Magallana gigas* adjust their energy metabolism across a broad pH range (7.0–8.1). A 0.1-unit decrease in pH (from 8.2 to 7.5) reduced mussel oxygen consumption by 10–20%. Notably, *M. galloprovincialis* respiration remained stable (9.15–9.38 μg O_2/(g dry tissue·h)) within the pH range of 7.2 to 7.5, suggesting metabolic compensation in this range.

Bivalves counteract acidification by upregulating proton pumps, such as V-type H^+-ATPase, to maintain intracellular pH and by increasing bicarbonate ion (HCO_3^-) transport to the calcification site (Wright-Fairbanks *et al*., 2025). These energy-intensive processes can consume 30–50% of the larval energy budget. Under hypoxic conditions (dissolved oxygen < 2 mg/L), this increased energy demand leads to unsustainable biomass reductions of 17–22% in *C. virginica*. Multi-stressor experiments demonstrate that the combined effects of hypoxia and acidification reduce condition indices (meat-to-shell ratio) by 35%, indicating a preferential allocation of energy toward shell maintenance over soft tissue growth (Ledezma, 2024). In another study, blue mussels (*M. edulis*) tolerate moderate pH levels (7.1–8.1) but with metabolic costs. At pH 7.7, they increase energy allocation to their gills and hemocytes while maintaining ATP synthesis (Guo *et al*., 2021). However, at pH 7.1, total adenylate pools and ATP levels decrease significantly. Adult oysters regulate ion levels more effectively than larvae but still exhibit reduced growth at pH levels below 7.8 (Boulais *et al*., 2017). Larvae, which lack robust ion regulation, depend on seawater carbonate and are therefore more vulnerable to pH decreases that adversely affect their growth (Wright-Fairbanks *et al*., 2025) (Table 1). The metabolic rate responses of bivalves to varying pH levels are complex and depend on several factors, including species-specific traits, the exact pH level, the duration of exposure, and interactions with environmental variables. While extreme acidification typically suppresses metabolism to conserve energy, moderate pH reductions can initially stimulate metabolic activity as organisms try to maintain homeostasis. Future research should investigate the molecular mechanisms underlying these metabolic responses and investigate acclimation or adaptation processes that improve bivalve resilience to ocean acidification.

Table 1: Effect of pH on energetic costs in bivalves.

Species	pH levels	Energetic parameter	Effect	Reference
Patinopecten yessoensis	8.0 (control) and 7.5	Energy reserves (Glycogen)	Decreased in adductor muscle but increased in the hepatopancreas.	Liao *et al.* (2019)
M. coruscus	8.1 (control) and 7.7	Energy demand	Significantly increased, indicating higher basal maintenance costs.	Shang *et al*. (2023)
M. gigas	8.0 (control) and 7.4	Energy demand	No change in total energy consumption during first-shell formation.	Vialova (2023)
M. coruscus	8.1 (control) and 7.7	Cellular energy allocation	Significantly decreased, indicating a mismatch between energy demand and supply.	Shang *et al*. (2023)
C. gigas	8.1 (control) and 7.7	Cellular energy allocation	Decreased due to lower energy reserves and higher energy demand.	Frieder *et al*. (2017)
P. yessoensis	8.0 (control) and 7.5	Energy allocation	A large amount of energy was allocated to ion regulation (Na+/K+-ATPase) in the mantle and gill.	Liao *et al*. (2019)

[DOI: 10.22034/INJBIR.3.2.151]

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Respiration and oxygen consumption

Bivalve respiration responses to pH changes vary across species and environmental conditions. A decrease in pH often induces metabolic inactivity, resulting in a reduced rate of respiration (Zhao *et al*., 2017). This is often regarded as an adaptive strategy for conserving energy during periods of stress. For example, in Noble scallop (*Chlamys nobilis*), Mediterranean mussel (*M. galloprovincialis*), and blood clam (*T. granosa*), respiration rates decrease significantly as pH declines. Mussels exhibit a 10–20% reduction in oxygen consumption for every 0.1 unit decrease in pH between 8.2 and 7.5, with a sharp drop at pH 7.0. This suppression of aerobic metabolism is thought to enhance survival under acidification stress (Liu and He, 2012).

While some studies report increased respiration under acidified conditions, this is often linked to the elevated energy expenditure required to maintain acid-base balance and support other physiological processes (Shang *et al*., 2023). For instance, the larvae of the California mussel (*Mytilus californianus*) exhibited a two to threefold increase in respiratory activity at an approximate pH of 7.4. Similarly, adult blue mussels (*M. edulis*) demonstrated increased oxygen consumption as pH decreased (Waldbusser *et al*., 2015). A transient increase in oxygen consumption was also observed in *M. galloprovincialis* and Pacific oysters (*M. gigas*) at pH 7.7, possibly indicating an initial stress response preceding metabolic depression (Vialova, 2023).

Some bivalves maintain stable respiration rates despite decreased pH levels. For example, the pearl oyster (*Pinctada fucata*) and the green-lipped mussel (*Perna viridis*) exhibit no significant change in oxygen consumption between pH 8.1 and 7.4 (Liu and He, 2012). This suggests that certain species may be more resilient to acidification, potentially by prioritizing metabolic stability over processes such as growth (Table 2).

Table 2: Effect of pH on metabolic costs in bivalves.

Species	pH levels studied	Metabolic parameter	Effect	Reference
T. granosa	8.1 (control), 7.8, 7.6 and 7.4	Respiration rate	Significantly reduced with declining pH, indicating suppressed aerobic metabolism.	Zhao *et al*. (2017)
C. nobilis	8.1 (control), 7.7 and 7.4	Respiration rate	Significantly lower at pH 7.4.	Liu and He (2012)
M. californianus (larvae)	8.3 to 7.4	Respiration rate	Elevated at very low pH (~7.4); no change between pH 8.3 and 7.8.	Waldbusser *et al.* (2015)

Species	pH levels studied	Metabolic parameter	Effect	Reference
M. galloprovincialis	8.1 to 7.0	Respiration rate	Decreased by 10-20% per 0.1 unit drop (pH 8.2-7.5); stable from pH 7.5 to 7.2, then dropped at pH 7.0. Some studies report metabolic depression at pH 7.3.	Vialova *et al*. (2023)
C.gigas	8.1 to 7.0	Respiration rate	Decreased by 10-15% per 0.1 unit drop, reaching a minimum at pH 7.2-7.0.	Frieder *et al*. (2017)
P. fucata and *P. viridis*	8.1 (control), 7.7 and 7.4	Respiration rate	No significant effect.	Liu and He (2012)

Feeding and excretion rates

The filtration rate of bivalve mollusks, a critical factor influencing their growth, health, and ecological role, is highly sensitive to pH levels. Both natural variations in pH and human-induced changes, such as ocean acidification, can significantly affect their feeding efficiency. Bivalve filtration is influenced by pH because these animals respond both physiologically and behaviorally to changes in their chemical environment, particularly to maintain the acid-base balance of their haemolymph when external seawater pH fluctuates (Islam *et al*. 2020; Tsear 2021). Research demonstrates that the filtration capacity of bivalves exhibits a unimodal relationship with pH levels, reaching its peak at an optimal threshold rather than following a linear pattern. For example, the freshwater pearl mussel *Lamellidens marginalis* filters significantly faster at pH 8.0 than at pH 7.5 or 8.5 (Islam *et al*. 2020). Loayza-Muro and Elias-Letts (2007) observed that the freshwater mussel (*Anodontites trapesialis*) filtered most effectively at pH 8.0, with filtration rates decreasing significantly under more acidic conditions. Similarly, the thick-shelled mussel (*M. coruscus*), exhibit a significant reduction in clearance rate at noble scallops, green-lipped mussels (*P. viridis*), and blood clams (*T. granosa*) at lower pH levels (Liu and He, 2012; Zhao *et al*., 2017; Shang *et al*,. 2018). Reduced feeding can limit the energy available for vital physiological processes, including acid-base regulation and biomineralization (Zhao *et al*., 2017). Conversely, pearl oysters exhibited increased clearance rates at a pH of 7.7 (Liu and He, 2012). Reduced feeding due to ocean acidification is a critical sublethal effect that limits a bivalve's energy intake, potentially weakening growth, reproduction, and stress resilience (Gazeau *et al*., 2013) (Table 3).

[DOI: 10.22034/INJBIR.3.2.151]

Table 3: Bivalve filtration rate changes under ocean acidification.

Species	pH Range tested	Filtration rate response	Reference
T. granosa	8.1 (control), 7.8, 7.6 and 7.4	Significantly decreased with declining pH.	Zhao *et al*. (2017)
L.marginalis	7.5 to 8	Significant increase	Islam *et al*. (2020)
M. galloprovincialis	7.5-8.2	Decrease (10-20% per 0.1 pH unit)	Liu and He (2012)
M. galloprovincialis	7.2-7.5	No significant change	Vialova (2023)
C. nobilis	8.1 (control), 7.7 and 7.4	Decreased significantly at lower pH levels.	Liu and He (2012)
P. viridis	8.1 (control), 7.7 and 7.4	Decreased significantly at lower pH levels.	Liu and He (2012)
P. fucata	8.1 (control), 7.7 and 7.4	Rate was highest at the intermediate pH of 7.7.	Liu and He (2012)
Abra alba	7.2–8.2	No significant effect of pH observed	Vlaminck *et al*. (2022)

Acidic conditions (low pH) induce stress in bivalves, resulting in tissue irritation and a protective valve closure response through adductor muscle contraction (Loayza-Muro and Elias-Letts 2007). Valve closure significantly reduces water pumping and filtration. Addressing internal acidosis requires energy, which may stop filter feeding by diverting energy away from ciliary activity (Shang *et al*,. 2018).

The effect of pH on filtration rate often depends on various environmental factors, leading to complex interactions. For example, rising temperatures can exacerbate the effects of pH changes. For example, Vlaminck *et al*. (2023) found that warmer temperatures intensified the negative impacts of acidification on white furrow shell (*Abra alba*), leading to increased mortality and a reduced contribution to sediment biogeochemistry. The harmful effects of a lowered pH level are increased by the presence of pollutants. For instance, the decreased clearance rate of *M. coruscus* at low pH was further intensified by exposure to nano-ZnO particles (Shang *et al*., 2018), illustrating that multiple stressors can interact synergistically to exceed an organism's physiological capacity. A bivalve's energy intake from food influences its resilience to pH stress. Tsear (2021) observed reduced clearance rates under acidified conditions and suggested that prolonged exposure, coupled with decreased energy intake, could adversely affect their health and aquaculture potential.

Bivalve filtration efficiency is primarily influenced by water pH, with most marine and freshwater species exhibiting optimal filtration under slightly alkaline conditions. Ocean acidification induces physiological stress and reduces feeding activity, with species-specific responses that are further intensified by rising temperatures and pollutants.

Ammonia excretion indicates the catabolism of proteins and amino acids. Liu and He (2012) found that excretion

[DOI: 10.22034/INJBIR.3.2.151]

rates were significantly lower at pH 7.4 for *P. fucata*, *C. nobilis*, and *P. viridis*, suggesting reduced amino acid catabolism. This reduction may reflect metabolic adjustments that conserve energy and minimize the production of nitrogenous waste under pH stress. Conversely, blood clams exhibited elevated ammonium excretion at lower pH values, indicating increased protein utilization for energy (Zhao *et al*., 2017). This reduction may reflect metabolic adjustments that conserve energy and minimize the production of nitrogenous waste under conditions of pH stress.

Conclusion

Bivalve physiological responses to pH stress vary across marine, freshwater, and estuarine environments. Fluctuations in pH, particularly acidification, negatively affect bivalve physiology by impairing growth, calcification, metabolism, and feeding. Marine bivalves are highly sensitive to even slight decreases in pH, resulting in reduced survival rates and disrupted energy allocation. In contrast, freshwater species exhibit greater tolerance due to evolutionary adaptations. Larval and juvenile stages are especially vulnerable, often displaying developmental abnormalities, reduced growth, and increased mortality. Future research should focus on the molecular mechanisms underlying metabolic and physiological responses, investigating long-term acclimation and adaptation processes, and examining the combined effects of multiple environmental stressors.

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