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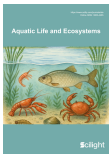

Review

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Stress Physiology and Aquaculture Adaptation of *Eleutheronema tetradactylum*: A Review

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Abstract: The expansion of fourfinger threadfin *Eleutheronema tetradactylum* aquaculture in southern China is limited by physiological factors. Environmental stress and oxygen requirement can be lethal factors in routine management. This review aims to address the effects of temperature, salinity, ammonia, handling stress, and density on *E. tetradactylum*. Thermal extremes, particularly low-temperature stress, can impact redox homeostasis and cause metabolic changes. Salinity outside the optimal range of 12–15‰ can increase the energetic cost of osmoregulation and reduce digestive enzyme activity. Ammonia can damage tissues through inflammatory and oxidative pathways, but its effects vary with salinity. Handling and crowding can increase physiological load by activating the hypothalamic–pituitary–interrenal axis and thereby influence immunity and the gut microbial community. These results point to a practical requirement for *E. tetradactylum* farming. Physiological indicators should be linked with water quality control and multi-omics interpretation to manage stress risk.

Keywords: *Eleutheronema tetradactylum*; physiological stress; temperature; salinity; ammonia–nitrogen stress; handling stress

1. Introduction

In *E. tetradactylum*, the practical bottleneck for aquaculture is no longer simply limited by hatchery production. A more persistent question is how reliably fish can be kept within a stable physiological range as culture systems become denser and more technically complex. This polynemid fish inhabits warm coastal waters of the Indo–West Pacific, and its flesh quality, growth potential, and high market price have supported growing interest in marine aquaculture in southern China and Southeast Asia (Figure 1) [1–3]. In China, production has begun to cluster in Fujian, Guangdong, and Hainan Provinces across more than 1200 km of coastline [4–6]. With artificial breeding techniques now more established, farming has expanded from traditional ponds into high-density land-based recirculating aquaculture systems (RAS) and offshore deep-water cages [7,8]. These systems can increase output, but they also make water-quality shifts, density effects, transport, and handling more frequent and more abrupt. Mortality in culture should therefore be read not only as a final production loss, but also as

evidence that physiological tolerance has been exceeded. Clarifying the basis of this vulnerability is necessary if the species is to develop from a promising candidate into a stable aquaculture resource [9–11].

Figure 1. *Eleutheronema tetradactylum* (Shaw, 1804). Original photograph by the authors.

The physiological basis for this vulnerability is increasingly apparent. *E. tetradactylum* combines high stress sensitivity with high oxygen demand; its stress responsiveness has been reported to approach that of active pelagic fishes such as yellowfin tuna (*Thunnus albacares*) [12,13]. Capture, deterioration in water quality, and photoelectric stimuli can disturb metabolic balance in this species under both routine and experimental conditions [14]. Acute hypoxia is a measure to detect the stress responses in serum lactate dehydrogenase (LDH) and creatine kinase (CK) activities, which reflect cardiac and muscular injury in anaerobic metabolism [15–17]. During ammonia stress, SOD elevation is considered a compensatory antioxidant defense, as MDA accumulation can lead to lipid peroxidation and oxidative injury. In practice, these responses are indicative of the operational stress of *E. tetradactylum* during ordinary aquaculture operations [18].

Recent literature has documented how *E. tetradactylum* responds to changes in temperature, salinity, ammonia, and seawater acidification. Species-specific responses are strong for short-term changes in tissue integrity, oxidative status, ion regulation, endocrine activity, and metabolism. However, mechanisms have not been tested in *E. tetradactylum*. This species can serve as a model for marine teleost and euryhaline aquaculture species for future research to understand how environmental factors affect metabolic responses and growth performance in aquaculture. This review uses observations in *E. tetradactylum* to integrate findings on major aquaculture species for stress-related responses (Table 1). In the current literature, we identified four response axes, including redox imbalance, HPI-axis activation, immune dysregulation, and altered energy allocation. We present these interactions and their aquaculture implications in Figure 2.

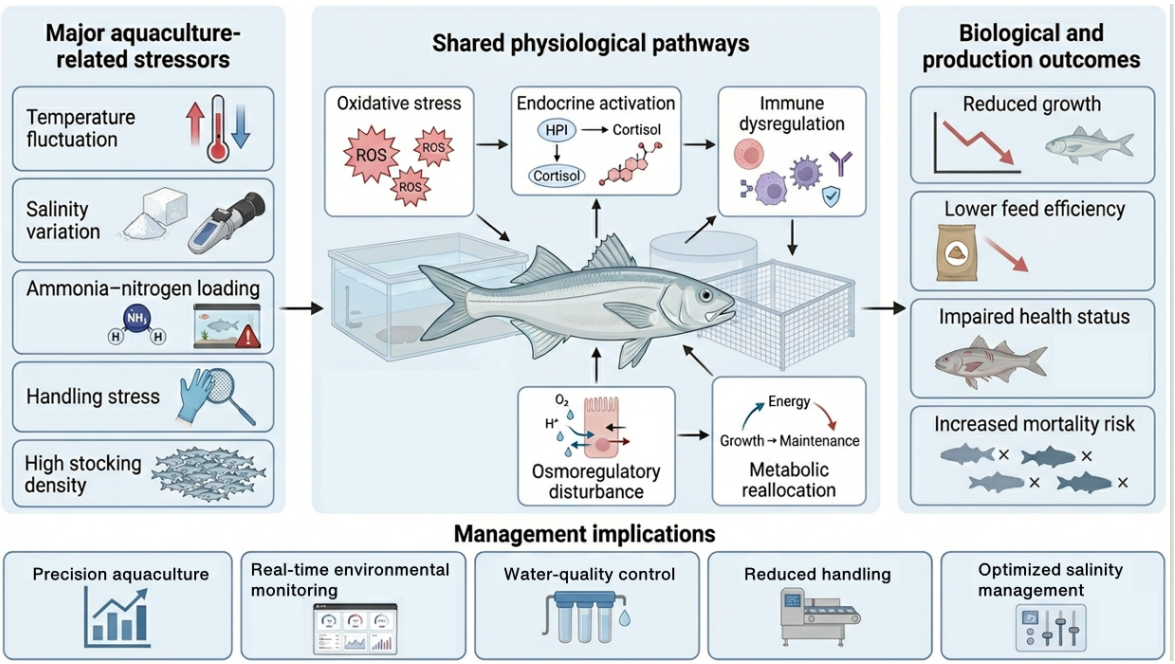

Figure 2. Conceptual framework of physiological stress and management strategies in *E. tetradactylum* aquaculture.

Table 1. Summary of physiological responses of *Eleutheronema tetradactylum* to major aquaculture-related stressors.

Environmental Factor/Topic	Species (Length/Weight)	Experimental Conditions/Stress Level	Exposure Duration	Sampled Tissues/Measured Parameters	Key Conclusion	Reference
Temperature (low-temperature stress)	Juveniles; TL 9.63 ± 0.81 cm; BW 8.54 ± 1.62 g	Acute low-temperature stress	24 h	Liver, muscle, gill histology	Low-temperature stress induced structural damage, including hepatocyte vacuolation and deformation of gill lamellae.	[16]
Temperature (oxygen consumption)	Juveniles; TL 9.8 ± 0.3 cm; BW 10.1 ± 1.4 g	Different temperature gradients	Continuous monitoring	Oxygen consumption rate, asphyxiation point	Oxygen consumption increased with temperature; critical asphyxiation thresholds were identified at different temperatures.	[6]
Air exposure	Juveniles; TL 11.41 ± 0.73 cm; BW 15.54 ± 2.62 g	Acute air-exposure stress	0–24 h	Tissue structure, oxidative stress indicators	Air exposure increased MDA levels and produced tissue damage consistent with oxidative stress.	[17]
Handling stress	Juveniles; TL 11.52 ± 0.68 cm; BW 15.82 ± 2.74 g	Acute handling (simulated capture)	0–48 h	Liver histology, antioxidant enzymes (SOD, CAT, etc.)	Handling triggered stress responses; hepatic antioxidant enzyme activities showed an initial increase followed by a decline.	[18]
Salinity tolerance	Fertilized eggs and larvae (TL 2.0 ± 0.2 mm)	Salinity gradients (0–40‰)	Embryonic and larval stages	Hatching rate, larval survival	Optimal salinity ranges and tolerance limits for embryonic and larval development.	[19]
Salinity (juveniles)	Juveniles; TL 8.5 ± 0.5 cm; BW 6.2 ± 1.1 g	Different salinity levels	Short- and long-term exposure	Survival rate, gill morphology	Both high and low salinity altered gill filament morphology, impairing osmoregulatory capacity.	[20]
Freshwater stress	Juveniles; TL 10.51 ± 0.77 cm; BW 11.05 ± 2.45 g	Acute freshwater challenge	0–72 h	Gill, heart, spleen, liver histology	Freshwater exposure caused histopathological alterations and disrupted osmotic balance.	[21]
Hypoxia stress	Juveniles; TL 10.74 ± 0.61 cm; BW 11.89 ± 2.08 g	Acute hypoxia	0–24 h	Spleen and heart histology	Hypoxia induced tissue congestion and cellular degeneration in circulatory organs.	[22]
Hypoxia stress	Juveniles; TL 11.23 ± 0.84 cm; BW 12.56 ± 2.31 g	Acute hypoxia	0–24 h	Gill and liver histopathology	Gill lamellar hyperplasia and hepatic sinusoidal dilation were observed; the liver was highly sensitive to hypoxia.	[23]
Development and histochemistry	Larvae (2 cm), juveniles (10 cm), adults (26 cm)	Different developmental stages	Throughout development	Gastrointestinal mucous cells (AB–PAS staining)	The type and distribution of gastrointestinal mucous cells changed progressively with development.	[24]

2. Physiological Responses to Thermal Stress

Temperature is a risk factor in *E. tetradactylum* farming when coastal farming systems experience rapid cooling, heat spells, or abrupt seasonal transitions. Temperature is a primary factor shaping growth, development, and reproduction [18,19] and impact enzyme activity, and cellular homeostasis in ectothermic organisms [25–30]. Climate-related events increase the chance of coastal heatwaves and winter cold spells [31,32]. In most aquaculture species, thermal disturbance may alter energy metabolism, antioxidant capacity, immune function, and the structure of the intestinal microbial community.

In *E. tetradactylum*, this risk of thermal stress is related to the lack of specialized thermoregulatory structures [33]. Unlike yellowfin tuna (*Thunnus albacares*), which can maintain a high temperature in tissues through endothermy and countercurrent heat exchange, *E. tetradactylum* depends on water temperature for metabolic performance [13]. Abrupt winter cooling has been reported to suppress nonspecific immune factor activity, increase vulnerability to pathogenic microorganisms, and may induce metabolic shock [34]. Temperature stress can also disturb neuroendocrine regulation, slow growth and reduce feed conversion efficiency [14,35]. For farming, thermal stability is therefore a management concern as well as a physiological one.

Among molecular indicators, heat shock proteins (HSPs) provide the clearest evidence of rapid thermal response in *E. tetradactylum* [36]. These molecular chaperones assist the refolding of denatured proteins and limit nonspecific aggregation of damaged polypeptides [37–39]. When water temperature rises acutely from 28 °C to 34 °C, hepatic hsp70 mRNA expression increases in a pulse-like pattern, generally peaking within 2–4 h. The heat response is therefore rapid, whereas low-temperature exposure appears to elicit a weaker hsp70 response and is often accompanied by metabolic suppression. For this tropical species, cold exposure may thus be the more difficult short-term challenge, although the timing and magnitude of HSP responses still need to be compared across developmental stages and culture conditions [14,35,40]. Similar findings from other marine fishes help to establish the pattern, but the model needs data collected from *E. tetradactylum*.

Deviation from the apparent optimal temperature of 28 °C also influences the antioxidant system in *E. tetradactylum* [9,14,41]. In the liver, acute exposure to 34 °C increases SOD from 85.0 U/mg prot to 155.0 U/mg prot to neutralize excess superoxide radicals [13,14], but such an increase cannot prevent oxidative damage. If the subsequent detoxification by enzymes such as CAT is behind ROS production, lipid peroxidation cannot be avoided [18]. In fact, when the MDA concentration at 34 °C reached 5.8 nmol/mg prot, the high temperatures can change the tissue antioxidant capacity [13,14]. Antioxidant indices are best interpreted as dynamic responses over time, rather than as single-point measurements.

Temperature-related stress may be associated with changes in the intestinal microbiota. At 28 °C, the intestinal environment of *E. tetradactylum* remains relatively stable. However, when temperature deviates from this level, changes in mucus secretion and dissolved oxygen may alter the conditions for gut bacteria [42,43]. For example, thermal stress can reduce the Shannon diversity index from 5.2 to 3.2. The taxonomic shift was also recorded. For instance, Proteobacteria became more abundant, while Vibrio increased from less than 5% to 30–45% under high-temperature stress. Such a change is substantial in a cultured species because reduced microbial diversity and *Vibrio* enrichment may affect digestion, mucosal defense, and susceptibility to infection. Even so, the consequence of thermal dysbiosis to systemic inflammation or mortality has not been clearly found in *E. tetradactylum* [34,43]. Taken together with the responses to salinity, ammonia, and handling stress, these findings suggest that gut microbial disturbance may be a downstream consequence of environmental stress that reduces immunity.

3. Physiological Responses to Salinity Stress

In *E. tetradactylum* aquaculture, salinity determines how much energy is allocated to ion regulation. In other marine fishes, salinity also influences species distribution, growth, and survival [44–46]. Osmotic balance accounts for 10–50% of metabolic energy [47]. When external salinity moves away from the isosmotic point, the gills, kidneys, and intestine need to coordinate osmotic regulation [48]. Gill Na^+/K^+-ATPase (NKA) is crucial to energy allocation as it drives active ion transport and maintains intracellular homeostasis [49]. If salinity change is abrupt, the osmoregulatory load may trigger ROS production, lipid peroxidation, immune disruption, and metabolic imbalance [50,51].

As a euryhaline fish, *E. tetradactylum* exhibits growth and developmental processes linked to salinity changes in estuarine environments [13]. Performance near a salinity range of 12–15‰ is better as NKA activity and the energetic cost of osmoregulation are low [9]. Growth performance, feed conversion efficiency, and digestive enzyme activity are also higher under these conditions, as less energy is expended to ion transport [52]. Movement away from this range increases osmoregulatory demand, raises cortisol levels, and induces compensatory changes through enhanced chloride-cell activity [53]. Salinity tolerance can also change with developmental stages. Larvae

generally tolerate relatively high salinity, whereas juveniles appear to benefit from salinities closer to the isosmotic range [19,20]. These stage differences must be considered because a salinity regime suitable for seed production may not be suitable for juvenile grow-out.

Salinity stress can cause oxidative injury and osmoregulatory adjustment in *E. tetradactylum*. Once external salinity moves beyond the range of species tolerance, liver and gill tissues will increase ROS production, MDA accumulation, and loss of membrane integrity [54]. The early rise in SOD and CAT activities, therefore, needs attention because it marks activation of antioxidant defenses [9]. Similar links among ion-regulatory effort, antioxidant response, and growth change have been reported in other euryhaline marine teleosts. For farm management, unresolved issues include identifying the salinity threshold at which *E. tetradactylum* shifts from compensation to disruption, particularly when salinity fluctuates with ammonia accumulation, hypoxia, or handling stress.

4. Physiological Responses to Ammonia Stress

At a high stocking density in *E. tetradactylum* aquaculture, ammonia is a major parameter for water quality management because it develops from feeding, waste retention, and limited water exchange [40–46]. In water, total ammonia nitrogen is partitioned into unionized ammonia (NH_3) and ionized ammonium (NH_4^+). NH_3 is more toxic because it can easily cross the gill epithelium. After entering the blood circulation system, NH_3 may disturb neural transmission and intracellular pH balance [40,55]. Gill filament damage will immediately reduce respiratory efficiency. As exposure is prolonged, inflammatory and oxidative processes are activated, and antioxidant enzymes such as SOD and CAT may decrease. Therefore, ammonia accumulation in culture water can gradually develop into tissue injury and metabolic dysregulation [40–48].

In *E. tetradactylum* aquaculture, ammonia toxicity is associated with salinity [13]. Within the tested range, salinity and ammonia toxicity are negatively related, with higher salinity reducing ammonia-induced physiological damage [56]. At a salinity <5‰, active ion transport supports plasma osmotic balance, leaving less physiological capacity to cope with ammonia exposure. Gill histology is consistent with this energetic trade-off. Under high ammonia, low salinity can increase gill epithelial cell height and increase intercellular spaces. Within the plasma isosmotic range (~12–15‰), osmoregulatory demand is lower and gill structure is comparatively better protected. Competitive inhibition at branchial ion-transport sites offers a possible explanation for the interaction between salinity and ammonia, as Na^+ and Ca^{2+} can compete with NH_4^+ and reduce ammonia uptake from water [9,13].

Molecular and metabolic results point in the same direction to explain the mechanism of salinity and ammonia interaction on ammonia toxicity [57,58]. At equivalent ammonia concentrations, the *E. tetradactylum* at 15–25‰ salinities exhibits weaker induction of TNF-α and IL-6r than at lower salinity [59]. Muscle SOD activity is also high at elevated salinity and gives the tissue more capacity to remove ROS during ammonia exposure and reduces lipid peroxidation injury in muscle fibers [60,61]. From an aquaculture perspective, salinity adjustment may act as a partial buffer against ammonia stress.

Behavioral and swimming performance data also suggest an interaction between salinity and ammonia in aquaculture settings. Under isosmotic or moderately high salinity, ammonia-exposed *E. tetradactylum* maintains higher muscle glycogen reserves and a more stable critical swimming speed (Ucrit) [59]. Such reserves may help preserve escape capacity and short-term performance during episodes of elevated ammonia–nitrogen levels following overfeeding or waste accumulation. Comparable ammonia-related oxidative damage, inflammatory activation, and ionoregulatory disturbance have been reported in other freshwater and marine fishes. In *E. tetradactylum*, these effects may carry greater practical value because high metabolic demand leaves little room for additional environmental fluctuation.

5. Physiological Impacts of Aquaculture Density and Handling Stress

Stocking density and handling are two important factors in E. tetradactylum farming because they are repeatedly encountered under normal culture conditions, and water-quality changes can rapidly affect fish behaviour and stress responses [51,62]. During grading, transfer, or harvest, fish may be crowded for short periods, and dissolved oxygen can be a stressor; short-term holding, HPI-axis activation, density stress, and oxidative stress are commonly involved in these handling-related responses [52,53,63,64]. If biomass continues to increase, competition for oxygen and the accumulation of waste products may create a chronic stress background [65]. Handling adds a short disturbance, since capture and tank transfer can rapidly affect metabolic balance and immune status [10,65]. Similar responses have been found in other cultured marine teleosts, including endocrine activation, oxidative imbalance, and poor production performance. For *E. tetradactylum*, a crucial issue is the limited recovery margin when crowding and handling repeatedly occur during intensive farming.

In this species, high density, together with frequent handling, is associated with oxidative damage, metabolic disorders, and mortality under intensive farming [11]. The main systemic route is activation of the hypothalamic–pituitary–interrenal (HPI) axis [65]. Stress perception stimulates hypothalamic release of corticotropin-releasing hormone (CRH), pituitary secretion of adrenocorticotropic hormone (ACTH), and cortisol release from interrenal cells in the head kidney [63]. A short cortisol pulse is a sign of acute stress. The culture problem emerges when repeated crowding keeps the HPI axis active, because elevated cortisol may suppress immune function and redirect energy from growth and reproductive development [9].

Hematological and metabolic variables show how rapidly these disturbances are related to energy use. During harvesting or crowding, blood glucose may rise as cortisol promotes hepatic glycogenolysis, thereby supplying energy for escape behavior. If swimming effort becomes intense, muscle anaerobic glycolysis increases and blood lactate rises, leading to acid–base balance changes. *E. tetradactylum* may also increase hemoglobin concentration and hematocrit through splenic contraction to improve oxygen transport during acute stress. These measures are necessary when interpreted alongside behavior and water-quality conditions, because a single parameter is unlikely to identify the cause [9,13].

In farming conditions, behavioral changes usually occur before physiological disruption can be detected in *E. tetradactylum* [64]. At high stocking densities, feeding often becomes less stable because cortisol-related stress interferes with appetite, reducing feed intake and feed conversion efficiency. Reduced swimming may further disturb schooling behavior, increase aggressive interactions, and cause body-surface injuries, creating more opportunities for pathogen entry [54]. Once these signs appear together, density stress should no longer be viewed only as a growth-performance problem. It is more appropriately treated as an early sign of declining health status and a warning of mortality risk.

6. Future Directions

Recent literature has identified the main stress factors affecting *E. tetradactylum*, but research on improving culture management remains limited. Most studies examine short-term responses to a single stressor, whereas farm losses often occur when several manageable variables shift simultaneously. The next phase of research, therefore, needs to ask more practical questions. For instance, which stress combinations can prevent fish from injury, which life stage can lose physiological balance first, and which indicators can warn farmers before mortality begin? Reproductive characteristics should also be considered when evaluating broodstock management and developmental-stage sensitivity in *E. tetradactylum* [66].

Multifactorial stress occurs in practical farming situations, unlike a set of isolated laboratory challenges. Temperature, dissolved oxygen, and ammonia are likely to interact during real farming incidents. For instance, warming increases oxygen demand, hypoxia limits aerobic metabolism, and waste accumulation raises ammonia exposure. We should combine these factors to yield information for predicting survival and performance. In land-based RAS, high stocking density, ammonia accumulation, pH fluctuations, and acidification require a specific experimental design to identify the main impact factors, particularly regarding immune defense. In offshore deep-water cages, sudden cold surges, salinity shifts, runoff, and hypoxia are important parameters because they can disrupt metabolic homeostasis over short timescales.

Future studies need to focus on which stress first becomes a health threat factor. Indicators such as LDH, SOD, and MDA are useful, but they are often shown after stress rather than before. Transcriptomic analysis may help identify early responses in the liver, gills, heart, or other target tissues during thermal shock, hypoxia, or ammonia exposure. Metabolomic profiling would be relevant for *E. tetradactylum*, because high oxygen demand occurs when energy metabolism begins to shift toward anaerobic glycolysis. Microbiome data are useful for testing whether environmental disturbance leads to gut dysbiosis before inflammation; transcriptomic evidence of immune responses, pathogen-associated gut microbiome shifts, and feeding ecology may further help explain stress-related health changes in *E. tetradactylum* [60,67,68]. For these approaches to be useful in culture management, omics results need to be paired with physiological variables in farm assessment. Molecular signals should be used as warning information rather than as post-analysis markers.

Ontogenetic sensitivity remains in limited developmental stages, making it difficult to know whether eggs, larvae, juveniles, or adults are most vulnerable to a given stress condition. During development, *E. tetradactylum* changes enzyme activity, ion-regulatory capacity, digestive function, and behavior. Furthermore, salinity tolerance also differs between larval and juvenile stages. A more informative design would compare stress responses across different life stages. From an evolutionary perspective, the euryhaline background, life-history diversity, population connectivity, potential contaminant exposure, population organisation, and responses to extreme marine heatwave events may shape adaptive potential and farm-scale risk, while culture environments also alter

stress responsiveness [54,65,69,70]. Temperature-driven changes in fish production, heat-stress transcriptomic responses, low-temperature stress responses, and combined salinity-temperature effects should also be considered when evaluating environmental adaptability and culture risk [55,71–73]. To distinguish conserved teleost responses from vulnerabilities specific to *E. tetradactylum* require species-specific experiments under selected environment variables.

Precision aquaculture research will shift from device evaluation to decision-making. Because *E. tetradactylum* has high oxygen demand and low stress tolerance, real-time monitoring is required when measured variables can be linked to physiological risk. A practical target is to define warning thresholds for dissolved oxygen, ammonia, salinity, temperature, and handling, and then test whether management actions at those points reduce injury or mortality.

System-specific experiments need farm-scale validation. In RAS, the central question is how density, ammonia, pH, and oxygen demand interact over culture cycles. In deep-water cages, the concern is how abrupt cold events, salinity change, hypoxia, and handling interact during short high-risk windows. In any system, physiological indicators need to be evaluated as predictive tools. We should be informed of the changes in SOD, CAT, MDA, cortisol, LDH, CK, or Ucrit after stress occurs, and then use the pattern of these changes to predict future events.

7. Conclusions

The *E. tetradactylum* responds to aquaculture stress through a set of physiological pathways, including oxidative imbalance, HPI-axis activation, ionoregulatory adjustment, metabolic reallocation, immune disturbance, and behavioral change. Temperature and salinity variations are proximate factors that trigger changes in metabolic rate, osmotic demand, and energy allocation. Ammonia exposure adds tissue injury and inflammation, while handling and high stocking density can turn acute stress responses into a chronic physiological burden.

For aquaculture practice, local validation is required to apply these findings to *E. tetradactylum*. The suggestions are to keep salinity close to the isosmotic range, avoid abrupt temperature change, prevent ammonia accumulation through water-quality control, and reduce handling or crowding during routine operations. These measures can reduce stress risk, but a comprehensive management model for this species requires further research. The current research evidence is mainly based on short-term, single-stressor, and often juvenile-focused studies. Therefore, the thresholds for RAS, offshore cages, and different developmental stages remain uncertain. Future culture protocols for *E. tetradactylum* will be based on both physiological mechanism and farm-scale verification.

Author Contributions

L.Q.: conceptualization, methodology, investigation, writing—original draft preparation, writing—review and editing; S.L.: literature search, data curation, formal analysis, investigation, writing—original draft preparation; Y.O.: validation, resources, supervision, writing—review and editing; Z.M.: conceptualization, supervision, project administration, funding acquisition, writing—review and editing. All authors have read and agreed to the published version of the manuscript.

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Institutional Review Board Statement

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Informed Consent Statement

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Data Availability Statement

The datasets generated and analyzed during the current study are available from the corresponding author upon reasonable request.

Conflicts of Interest

The authors declare no conflict of interest.

Use of AI and AI-Assisted Technologies

During the preparation of this work, the authors used ChatGPT for language editing and grammar improvement. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

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