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## EXTRATERRESTRIAL AQUACULTURE: ITS CONCEPTUAL FOUNDATIONS AND SCOPE

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### Abstract

Extraterrestrial aquaculture (“space aquaculture”) is increasingly discussed as a distinct interdisciplinary research field at the intersection of aquatic biology, astrobiology, space systems engineering, and related space life and environmental sciences. This review focuses on how aquatic organisms and closed-loop aquatic systems respond to space-relevant constraints, particularly microgravity and cosmic radiation, within confined and resource limited operational settings. By synthesizing the available literature, including technical reports from space agencies and data from orbital missions, together with evidence from ground-based simulation studies, the article consolidates the conceptual foundations that motivate extraterrestrial aquaculture as a coherent field of inquiry. It also identifies evidence informed gaps in current research and outlines recommendations for future work, emphasizing candidate species selection and the definition of high-impact study areas relevant to sustaining life support functions in extraterrestrial habitats.

**Keywords:** Astrobiology, extraterrestrial aquaculture, candidate species selection, recirculating aquaculture systems (RAS), bioregenerative life support system (BLSS)

## Introduction

Extraterrestrial aquaculture, also referred to as space aquaculture, is defined as the controlled cultivation and managed rearing of aquatic organisms in environments beyond Earth's atmosphere, including spacecraft, orbital infrastructures, and engineered habitats established on extraterrestrial bodies. As an emergent interdisciplinary research domain, it integrates conceptual and methodological frameworks derived from terrestrial aquaculture, aquatic biology, astrobiology, space sciences, environmental physiology, radiation biology, space medicine, and space systems engineering. In tandem, it draws upon planetary sciences, particularly astrogeology and planetary geology, to delineate environmental boundary conditions, regolith-water interaction constraints, habitat shielding requirements, and in situ resource utilization architectures that define experimental feasibility and operational scalability beyond Earth (Przybyla, 2021; Brown et al., 2021; Duri et al., 2022)

Importantly, the field is not principally oriented toward the near-term realization of large-scale food production. Rather, its primary objective is the systematic interrogation of how aquatic organisms and water-dependent biological systems respond to the distinct physical, radiative, and operational stressors characteristic of space environments, including microgravity, partial gravity, chronic low-dose galactic cosmic radiation, solar particle events, confinement, isolation, and closed-loop resource governance (Przybyla, 2021; Abdullah et al., 2026). In this framing, extraterrestrial aquaculture functions as an experimental systems platform for quantifying multi-scale biological resilience, adaptive plasticity, and bioprocess stability under non-terrestrial boundary conditions (Blüm & Paris, 2002; Przybyla, 2023, Shelake et al. 2025).

Its strategic relevance has intensified as concurrent roadmaps for long-duration human spaceflight and sustained lunar and Martian surface operations have been articulated. Strategic planning documents from agencies such as NASA, ESA, and CNSA increasingly emphasize bioregenerative and hybrid life-support architectures as essential components of mission resilience and logistical autonomy (Arroyo et al., 2023 ; Poughon et al. 2021). These ambitions necessitate closed-loop biological infrastructures capable of operating under reduced gravity fields, elevated radiation flux, constrained resupply intervals, and strict mass-energy budgets (Fu et al., 2021; De Micco et al., 2023). Within this broader habitat metabolism, space aquaculture is best treated not as a peripheral food-production adjunct, but as a prospective aquatic bioprocess subsystem embedded within integrated life-support networks.

Relative to terrestrial systems operating under stable gravitational loading, open-atmosphere gas exchange, and comparatively redundant supply chains, extraterrestrial aquatic modules must function within altered gravity regimes, persistent ionizing radiation exposure, atmospheric confinement, and stringent material recycling imperatives (Przybyla, 2021; Herranz et al., 2013). The resulting deviations extend beyond organism-level stress responses. Reduced buoyancy-driven convection, altered hydrostatic gradients, and modified sedimentation dynamics reshape fluid-mechanical regimes and gas-liquid mass transfer characteristics (Beysens, 2022; Verbeelen et al., 2021). Concurrently, radiation-associated reactive oxygen species generation and DNA damage pathways can perturb cellular homeostasis, influence mutation rates, and affect long-term population stability (Herranz et al., 2013; Alekseev et al., 2022). Environmental constraints therefore co-determine biological performance and engineered architecture across interacting scales.

Accordingly, extraterrestrial aquaculture should be conceptualized as a coupled organism, environment and engineering domain rather than an organism-centered cultivation practice. In

closed aquatic habitats, biological responses are not limited to direct gravitational or radiative stimuli; primary physical perturbations induce secondary modifications in fluid stratification, boundary-layer thickness, shear distribution, gas dissolution kinetics, microbial consortial organization, and dissolved nutrient equilibria that diverge from terrestrial baselines (Drayer and Howard, 2014; Wuest et al., 2015; Fu et al., 2016). These physicochemical shifts propagate hierarchically, influencing membrane transport regulation, mitochondrial oxidative balance, transcriptional plasticity, developmental timing, metabolic flux partitioning, and behavioral regulation (Herranz et al., 2013; Fu et al., 2016; Alekseev et al., 2022). Therefore, conventional organismal indicators such as survival, growth efficiency, reproductive output, feed conversion ratio, or photosynthetic productivity cannot be interpreted independently of hydraulic configuration, water chemistry stability, microbial loop integrity, and cybernetic control architecture within life-support subsystems. Feasibility emerges from systems-level coupling, feedback coherence, and redundancy architecture rather than isolated biological tolerance (Przybyla, 2021; Fahrion et al., 2021; Przybyla, 2023) yet this systems entanglement remains insufficiently formalized in the current literature.

Despite a steadily expanding body of data from orbital missions, space station platforms, suborbital exposures, and altered-gravity analog systems, the evidence base remains structurally fragmented. Many investigations prioritize discrete biological endpoints, including behavioral adaptation, gametogenesis under microgravity, viability of dormant propagules, radiation tolerance thresholds, or cultivation feasibility of phototrophic microorganisms (Radzikowski, 2013; Alekseev et al., 2022; Przybyla, 2021). However, results are frequently reported without systematic mapping to subsystem-level operational metrics such as nutrient turnover kinetics, nitrogen cycling stability, biofouling trajectories, redundancy margins, failure-mode propagation, energy return ratios, or mission-duration scalability constraints (De Micco et al., 2023; Hu et al., 2022). In tandem, methodological distinctions between in-flight experimentation and ground-based simulation platforms are not consistently operationalized. Clinostats, random positioning machines, rotating wall vessels, magnetic levitation devices, and parabolic flight campaigns reproduce selected vector-averaged or transient gravity conditions but do not replicate radiation spectra, long-duration fluid redistribution, or habitat confinement variables in a fully coupled manner (Hammond and Allen, 2011; Wuest et al., 2015). The lack of standardized comparative criteria limits cross-platform inferential coherence and impedes cumulative synthesis; consequently, while biological resilience under individual stressors is increasingly documented, translation into reproducible, mission-relevant aquatic bioprocess performance remains under-theorized.

The interface between extraterrestrial aquaculture and Bioregenerative Life Support Systems is therefore structurally foundational. Within closed habitats, biological subsystems are expected to contribute simultaneously to oxygen regeneration, carbon dioxide assimilation, nitrogen mineralization, trace element cycling, water purification, and potentially edible biomass production (Blüm et al., 1995; Blüm et al., 2003; Häder, 2020). Aquatic modules including microalgae, cyanobacteria, crustaceans, mollusks, and finfish must thus be evaluated not solely for stress tolerance, but for compatibility with integrated mass-balance closure, waste assimilation fluxes, microbial ecological stability, pathogen containment, and long-term reliability engineering parameters (Voeste et al., 1999; Szydlowski et al. 2018; Häder, 2020; Liu et al. 2023; Amitrano et al. 2025). Although terrestrial Recirculating Aquaculture Systems provide a partial technological analogue for water recycling and biofiltration integration, extrapolation to extraterrestrial contexts requires explicit modeling of gravity-modulated hydraulic regimes, radiation-induced oxidative load, confinement-driven microbiome shifts, altered gas partial pressures, and stringent planetary protection and biosecurity constraints

(Przybyla, 2021; Fahrion et al., 2021; Amitrano et al., 2025). Terrestrial scaling laws derived from steady-state convection and atmospheric exchange cannot be linearly transposed to microgravity or partial-gravity habitats, where nonlinear coupling between physical transport and biological regulation becomes operationally decisive.

In response to these conceptual and methodological discontinuities, the present review advances a connectivity-centered systems synthesis of extraterrestrial aquaculture. The central problem addressed is the absence of a unifying analytical framework that links organismal adaptation, physicochemical boundary conditions, and engineered subsystem performance within a single operational architecture (Voeste et al., 1999 ; Alekseev et al. 2021 ; Przybyla, 2021) The scope is confined to aquatic modules conceptualized as integrated bioprocess systems functioning under space-relevant constraints. The review differentiates direct in-flight evidence from simulation-derived observations, maps biological endpoints onto subsystem-level performance variables, and identifies structural research gaps that constrain translational progression toward mission implementation. By consolidating insights from aquatic biology, astrobiology, environmental physiology, radiation science, and systems engineering, the objective is to reposition extraterrestrial aquaculture as a coherent, predictive domain grounded in integrative bioprocess modeling rather than descriptive biological enumeration (Przybyla, 2021; Fahrion et al., 2021; Blüm et al., 1995)

Advancing extraterrestrial aquaculture therefore requires a transition from siloed disciplinary outputs toward a formally articulated connectivity paradigm capable of resolving ontological fragmentation and epistemological discontinuity (Fig 1). This entails defining the operative unit of analysis across biological, physicochemical, and engineered strata; distinguishing structural configuration from functional output within closed aquatic modules; modeling emergent system behaviors under reduced gravity and radiation exposure; and establishing reproducible, quantitative metrics to evaluate system-level coupling, resilience thresholds, and reliability trajectories over mission-relevant timescales (Turnbull, 2018; De Micco et al., 2023) Embedding these principles within a network-informed, systems-analytic architecture enables extraterrestrial aquaculture to evolve from a dispersed set of experimental observations into a predictive science of aquatic bioprocess integration aligned with the operational imperatives of long-duration exploration missions and planetary habitation infrastructures.

## Material and Method

This work was designed as a systematic review targeting both the current evidence base and the conceptual foundations of extraterrestrial (space) aquaculture. The review integrates heterogeneous knowledge streams spanning (i) peer-reviewed scientific literature, (ii) technical and programmatic documentation released by national and international space agencies (e.g., NASA, ESA, JAXA, CNSA), and (iii) publicly documented outcomes of orbital and space-platform missions where aquatic organisms, aquatic microbiomes, or water-dependent bioprocess subsystems were investigated under space-relevant constraints. The methodological intent was not only to aggregate results, but also to evaluate how consistently biological findings are translated into system-level, mission-relevant performance variables within closed-loop life-support architectures.

A structured search was performed using *Google Scholar* as the primary discovery engine for peer-reviewed sources and citation chaining. Search strings combined controlled terms and

free-text variants of core concepts, including “space aquaculture,” “extraterrestrial aquaculture,” “microgravity,” “partial gravity,” “bioregenerative life support systems (BLSS),” “closed-loop,” “recirculating aquaculture systems,” “aquatic environmental physiology,” “radiation,” “spaceflight,” and organismal keywords (e.g., microalgae/cyanobacteria, crustaceans, mollusks, fish, aquatic microbiome). To increase recall while maintaining relevance, searches were iteratively refined via backward and forward citation screening of high-yield papers and key agency reports. Technical reports and mission documentation were retrieved from official agency repositories and mission archive portals when available, prioritizing primary documentation over secondary summaries.

Studies were considered eligible if they provided empirical or technically grounded evidence relevant to aquatic biological function and/or aquatic bioprocess performance under space-relevant conditions. This included (a) in-flight/orbital investigations, (b) suborbital or short-duration exposure studies, and (c) ground-based analogs explicitly designed to model one or more space constraints (e.g., altered gravity vectors, confinement, closed-loop water governance), provided that the study outcomes could be interpreted in relation to closed aquatic habitats or BLSS integration. Studies were prioritized when they reported endpoints that could be mapped to operational variables (e.g., growth/viability, reproduction, metabolic function, photosynthetic productivity, microbial stability, gas–liquid transfer implications, nutrient turnover) and/or when they specified engineering context (hydraulics, water chemistry control, biofiltration, monitoring/control architectures). Exclusion criteria included studies without clear linkage to aquatic systems, papers lacking interpretable methods/outcomes, purely speculative commentaries without technical grounding, and duplicated reporting of the same dataset without added analytical value.

Titles and abstracts were screened for relevance, followed by full-text assessment for final inclusion. When multiple publications reported overlapping experiments, the most methodologically complete or data-rich source was used as the primary reference, with companion papers retained only when they contributed distinct endpoints or system-level context.

For each included record, structured extraction captured: study type (in-flight vs analog), platform/constraint type (microgravity/partial gravity simulation, radiation exposure, confinement variables), organism/system component (e.g., phototrophs, heterotrophs, multi-trophic units, microbiome/biofilter elements), experimental duration, endpoints measured, and reported constraints relevant to closed-loop operation (mass/energy limitations, water chemistry control, gas exchange conditions, microbial management, and stability/reliability considerations). To support systems-level synthesis, outcomes were additionally coded into an interpretive matrix linking organismal responses (physiology, development, behavior, reproduction) to physicochemical boundary conditions (transport, stratification, dissolved gases, nutrients, redox dynamics) and engineered subsystem performance (control, stability, failure sensitivity, scalability).

Methodological guidance from the *Cochrane Handbook* was adopted as an organizing baseline for transparency in selection and synthesis (Higgins et al., 2024). Because the corpus spans diverse experimental paradigms in which conventional clinical risk-of-bias tools are not always directly transferable, the appraisal emphasized clarity of experimental control, adequacy of comparator conditions, constraints on confounding not replicated by analog platforms, measurement validity, and completeness of reporting. Evidence synthesis proceeded through a comparative framework that explicitly separated in-flight evidence from ground-based analog/simulation evidence, then analyzed concordance and divergence across these categories to identify where analog findings plausibly translate and where they do not. Beyond narrative aggregation, synthesis was oriented toward integrative coherence, operationalized as the degree to which a study’s biological endpoints can be meaningfully connected to subsystem-level

behavior inside closed-loop aquatic modules. This connectivity-centered evaluative stance follows the general logic of treating knowledge as structured associations across the organism, the environment, and system components (Turnbull et al., 2018; Kilic, 2019; Samet & Schank, 1984).

*Artificial intelligence (AI)*-supported tools were employed strictly as workflow facilitators. *AI* assistance was used to streamline literature discovery, organizational structuring, language refinement, and drafting support. However, all technical statements, interpretations, analytical linkages, and citations were independently verified against the underlying primary sources included in the final review corpus.

*Mendeley* was utilized for systematic reference management, annotation, literature organization, and internal cross-referencing during synthesis, while *Google Scholar* supported structured discovery and citation chaining. At no stage were *AI*-generated outputs treated as evidentiary content; all interpretive conclusions remained explicitly constrained to, and traceable within, the peer-reviewed and mission-documented sources incorporated in the study.

## Results

The compiled literature indicates that space-aquaculture-relevant evidence is distributed across three principal organism groups: aquatic vertebrates, primarily teleost fish models; aquatic invertebrates, particularly taxa with resistant dormant stages; and photosynthetic microorganisms evaluated as functional components of closed-loop systems. Across these biological categories, experimental approaches fall into two broad methodological classes: in-flight investigations conducted on orbital platforms and space stations, and ground-based simulations employing altered-gravity analog systems such as clinostats, random positioning machines, rotating wall vessels, centrifuge-based hypergravity devices, and related bioreactor platforms (Przybyla, 2021; Blüm, 1994; Blüm & Paris, 2001; Blüm, 2003; Häder, 2020; Berggren et al., 2025).

Within the fish-focused literature, microgravity effects are most frequently examined through endpoints related to orientation and locomotor control, early development, reproductive feasibility, and skeletal or otolith-associated responses. In-flight and controlled gravity studies demonstrate that fertilization, embryogenesis, and hatching can proceed under altered gravity conditions, while documenting measurable physiological modulation consistent with altered mechanosensory processing and bone-related pathways (Ijiri, 1995; Chatani et al., 2015).

Ground-based analog investigations provide complementary mechanistic resolution through controlled exposure windows and repeatable protocols; however, device heterogeneity and variation in effective gravity proxies limit strict cross-study comparability (Anken, 2003; Wuest et al., 2015; Aceto et al., 2015; Aceto et al., 2016; Edsall et al., 2014; Proshchina et al., 2021; Przybyla et al., 2023).

Historically, orbital fish studies began with Skylab missions, where mummichog minnows (*Fundulus heteroclitus*) and their eggs were flown to examine vestibular disorientation and early developmental responses in weightlessness. These experiments documented acute orientation disturbances followed by partial behavioral accommodation during continued exposure (Hoffman et al., 1977; NASA, 1977). Subsequent spaceflight programs, including Soviet missions, incorporated zebrafish (*Danio rerio*), establishing a longer vertebrate spaceflight record than often acknowledged (Takaoki, 2007; Proshchina et al., 2021). Microgravity-associated looping and orientation phenotypes have been experimentally linked

to otolith and vestibular function, supporting a sensorimotor integration interpretation (Takabayashi et al., 1995; Snyder et al., 1997; Horn, 2005).

Contemporary zebrafish research integrates quantitative video phenotyping with molecular and mineralization readouts, including gene-expression profiling and bone-formation assays under simulated microgravity, thereby increasing cross-study interoperability and mechanistic resolution (Aceto et al., 2015; Aceto et al., 2016; Rutter et al., 2020; Overbey et al., 2021). Developmental exposures in altered-gravity analogs have been associated with reduced ossification, stunted growth, and skeletal distortion detectable at later stages (Edsall et al., 2014).

Radiation effects have been examined independently of gravity manipulation. Zebrafish irradiation studies document durable molecular and epigenetic perturbations, including DNA-damage and methylation-linked signatures with developmental toxicity under proton or related exposures (Choi et al., 2015; Kamstra et al., 2018; Li et al., 2018). Similarly, accelerator-based neutron irradiation of European sea bass (*Dicentrarchus labrax*) eggs under dose regimes selected to approximate space-relevant conditions demonstrates preserved hatchability with measurable DNA-damage signals at defined developmental windows (Przybyla et al., 2025).

Within the JAXA lineage, medaka (*Oryzias latipes*) reproduction was directly demonstrated under microgravity, including mating, egg deposition, and normal hatching during Shuttle-era missions. Later experiments incorporated onboard centrifugation to separate gravity effects from background husbandry variables, documenting distinctive behavioral and physiological phenotypes under controlled gravity contrasts (Ijiri, 1995; Ijiri, 1998; Furukawa et al., 2020; Furukawa et al., 2021).

In parallel, launch-proxy vibration experiments and altered-gravity analog exposures in *D. labrax* embryos indicate preserved hatch rates under representative mechanical stress profiles and short-term gravity simulations, with modest modulation of developmental timing and selected immune transcripts (Przybyla et al., 2020; Przybyla et al., 2023).

Tilapia (*Oreochromis niloticus* and related taxa) appears frequently in mission concept analyses due to nutritional profile and culture robustness; however, publicly accessible in-orbit flight datasets remain limited relative to medaka or zebrafish lines (Gonzales Jr. et al., 2006).

Across vertebrate datasets, two patterns recur: mechanosensory and skeletal modulation under altered gravity is consistently documented, while early life-stage viability under controlled mission-like stressors is repeatedly demonstrated when exposure windows and husbandry parameters are carefully managed.

Invertebrate evidence is concentrated in taxa with resistant dormant stages, most prominently brine shrimp (*Artemia*) cysts. Shuttle-era missions and space-environment exposure studies report successful reactivation and post-flight developmental progression following spaceflight factors, supporting dormancy-based resilience framing (Spooner et al., 1994).

Additional studies emphasize survivability and post-exposure viability under spaceflight-related conditions rather than sustained production metrics (Gusev et al., 2007; Novikova et al., 2011; Radzikowski, 2013; Alekseev et al., 2022).

Bivalves are frequently proposed as filtration or protein nodes in integrated closed-loop concepts, but direct long-duration orbital cultivation datasets remain comparatively limited; altered-gravity effects are more commonly examined in ground-based larval orientation and feeding studies (Tang et al., 2021).

For photosynthetic organisms, the dominant evidence stream concerns cultivation feasibility and functional integration within closed-loop contexts, including oxygen production, carbon dioxide management, and nutrient cycling. Closed photobioreactor architectures compatible with orbital constraints have been tested using *Chlorella vulgaris* and *Arthrospira* strains within ISS-linked development lines, including MELiSSA-associated research (Lasseur et al., 2010; Detrell et al., 2021). Additional model systems include *Euglena gracilis* in Eu:CROPIS altered-gravity testing and *Chlamydomonas reinhardtii* in radiation and microgravity studies (Hauslage et al., 2018; Detrell et al., 2021).

Across these systems, engineering constraints emerge as primary determinants of performance under microgravity. Suppression of buoyancy-driven phase separation and altered bubble dynamics affect gas–liquid mass transfer efficiency, necessitating active air management, membrane-based exchange strategies, and phase-handling solutions in high-density cultures (Fili et al., 2020; Poughon et al., 2020; Detrell et al., 2021).

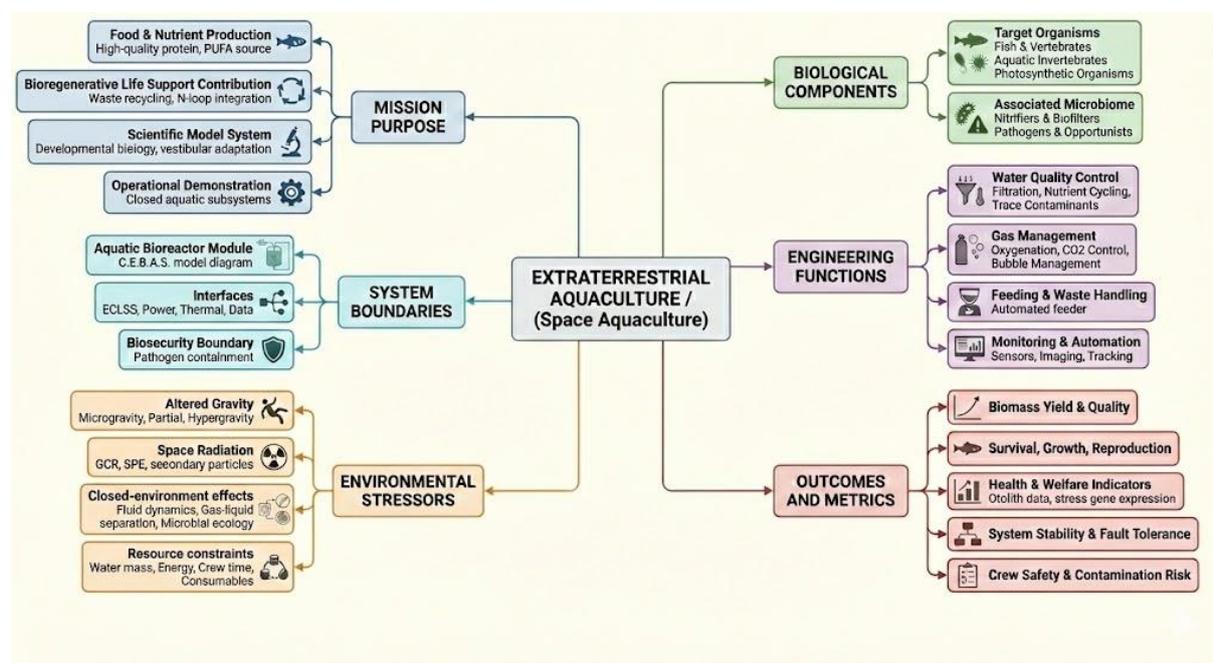
BLSS-oriented development lines evaluate phototrophic modules using integrated performance metrics, including oxygen-delivery stability, pH regulation, and control-loop robustness under continuous operation. In MELiSSA-based modeling and cultivation work, reactor mixing, light transfer, and gas-exchange constraints jointly define the operational envelope (Lasseur et al., 2010; Poughon et al., 2020; Ellena, 2024).

Across organism groups and platforms, reported biological endpoints are frequently linked to system behavior, including water-chemistry stability, microbial community dynamics, and mass-transfer characteristics involving oxygen, carbon dioxide, and nitrogen species (Herranz et al., 2013; Wuest et al., 2015; Poon, 2020; Ferranti et al., 2021; Vashi et al., 2023). Differences in shear regimes, mixing architectures, and gas-handling configurations between flight hardware and ground analog systems complicate direct cross-platform comparison.

Exposure duration, radiation spectra, device kinematics, and reporting granularity vary substantially across studies. Recommendations in the literature emphasize standardized disclosure of effective gravity proxies, shear parameters, illumination regimes, gas-transfer configurations, and bioreactor geometry to enable defensible comparative synthesis (Brungs et al., 2016; Topolski et al., 2022).

Overall, the evidence base documents organismal survival, reproduction, developmental progression, and photosynthetic productivity under selected space-relevant stressors. At the same time, methodological heterogeneity across flight and analog platforms constrains direct quantitative integration, reinforcing the need for harmonized reporting criteria tailored to aquatic bioprocess systems.

## Discussion



**Figure 1.** Figure 1. BLSS and Extraterrestrial Aquaculture (adapted from Blüm et al., 1995; Przybyla et al., 2021)

The evidence synthesized in this review demonstrates that extraterrestrial aquaculture has progressed beyond exploratory biological inquiry but has not yet achieved full operational maturity as an integrated subsystem science. Across vertebrates, dormant-stage invertebrates, and phototrophic modules, biological survivability under isolated space-relevant stressors has been repeatedly documented. However, subsystem-level predictability, controllability, and long-duration stability under closed-loop mission constraints remain insufficiently resolved (Przybyla, 2021). The principal contribution of this synthesis lies not in reiterating organismal tolerance but in reframing existing findings through a closed-loop systems perspective in which biological endpoints are interpreted as performance variables embedded within engineered architectures.

**Table 1.** Organizes aquatic taxa according to their functional role within prospective closed-loop bioregenerative architectures and summarizes existing space-relevant evidence alongside clearly defined research gaps. Inclusion reflects structured experimental priority rather than certification for extraterrestrial deployment.

Species	Functional Role	Existing Space-Relevant Evidence	Principal Evidence Gap	Structured Research Priority
<i>Danio rerio</i>	Mechanistic vertebrate model for gravity and radiation effects	Multiple microgravity and irradiation studies demonstrating sensorimotor and skeletal modulation (Takabayashi et al.,	Absence of long-duration closed-loop growth and density-dependent	Multi-generational stability studies with integrated nitrogen-cycle monitoring

<i>Oryzias latipes</i>	In-flight reproductive validation model	1995; Horn, 2005; Edsall et al., 2014; Aceto et al., 2015; Choi et al., 2015) Documented mating, fertilization, and hatching under microgravity (Ijiri, 1995; Ijiri, 1998; Furukawa et al., 2020; Furukawa et al., 2021)	performance data  Limited chronic skeletal and production-performance assessment	Long-duration growth, reproduction, and skeletal integrity analysis under controlled density
<i>Dicentrarchus labrax</i>	Translational aquaculture species	Altered-gravity and neutron irradiation analog data showing preserved hatchability with molecular perturbation (Przybyla et al., 2023; Przybyla et al., 2025)	Lack of multi-generational subsystem integration studies	Closed-loop RAS-type validation under factorial gravity–radiation designs
<i>Oreochromis niloticus</i>	High-robustness protein production candidate	Frequently cited in life-support system concept analyses (Gonzales Jr. et al., 2006)	Limited publicly available in-flight biological data	Pilot-scale controlled closed-loop performance evaluation
<i>Artemia</i> spp.	Dormant resilience and feed organism	Post-flight cyst reactivation and development documented (Spooner et al., 1994; Novikova et al., 2011; Alekseev et al., 2022)	Continuous biomass productivity under closed-loop conditions not evaluated	Long-duration trophic coupling and biomass-yield assessment
Bivalve larval models	Filtration and nutrient recovery node	Altered-gravity effects on larval orientation and feeding (Tang et al., 2021)	Absence of orbital cultivation and filtration-efficiency datasets	Controlled filtration-rate and nitrogen-removal performance testing
<i>Chlorella vulgaris</i>	Oxygen production and CO <sub>2</sub> assimilation	ISS-linked photobioreactor experiments and BLSS development (Lasseur et al., 2010; Detrell et al., 2021; Fili et al., 2020)	Gas-transfer efficiency constraints under chronic microgravity	High-density photobioreactor stability and phase-separation optimization

<i>Arthrospira</i> spp.	Nutritional biomass production	BLSS cultivation and modeling studies (Lasseur et al., 2010; Detrell et al., 2021)	Integrated long-duration subsystem validation lacking	Coupled nitrogen recovery and productivity-envelope characterization
<i>Euglena gracilis</i>	Altered-gravity phototrophic model	Eu:CROPIS gravity-related cultivation experiments (Hauslage et al., 2018)	Limited data on sustained productivity under closed-loop constraints	Gas-transfer stability and light-regime optimization under altered convection

Fish models, particularly zebrafish and medaka, consistently reveal a dual pattern. Altered gravity perturbs mechanosensory orientation and skeletal remodeling pathways (Horn, 2005; Edsall et al., 2014; Aceto et al., 2015; Aceto et al., 2016), whereas fertilization, embryogenesis, and hatching can proceed under microgravity when environmental control and husbandry variables are carefully regulated (Ijiri, 1995; Ijiri, 1998; Furukawa et al., 2020; Furukawa et al., 2021). This divergence suggests that gravitational alteration disrupts mechanical loading and vestibular integration before it compromises early developmental viability.

In aquaculture-relevant species such as *Dicentrarchus labrax*, simulated altered-gravity exposure and neutron irradiation under mission-representative dose regimes preserved hatchability while revealing measurable molecular perturbations (Przybyla et al., 2023; Przybyla et al., 2025). These results significantly reduce the translational distance between mechanistic vertebrate models and operational aquaculture species. Nevertheless, hatchability and short-term survival serve as threshold indicators rather than certifying subsystem robustness.

Operational feasibility within a bioregenerative life support architecture requires stable growth trajectories, reproducible feed conversion efficiency, predictable regulation of nitrogen flux, skeletal integrity under chronic altered loading, reproductive continuity across generations, and welfare compatibility at realistic stocking densities. Survivability under short-duration or staged exposures must therefore be interpreted as a necessary but insufficient condition for deployable aquatic modules.

Skeletal modulation under altered gravity is not an isolated biological anomaly but a systems-level constraint. Osteoclast activation in medaka reared aboard the International Space Station (Chatani et al., 2015) and persistent skeletal alterations in simulated microgravity zebrafish studies (Edsall et al., 2014) confirm that mechanotransductive pathways remain gravity sensitive. In confined aquatic habitats, altered swimming kinematics interact with engineered flow regimes, tank geometry, and density-dependent collision dynamics. Over extended periods, such mechanobiological and hydrodynamic coupling may result in gradual performance degradation rather than acute lethality (Amitrano et al., 2025). These reframing shifts vertebrate risk from short-term mortality to chronic efficiency erosion, which directly impacts mission-relevant productivity.

Radiation-mediated perturbations must be analytically separated from gravity-associated effects. Zebrafish irradiation studies document durable molecular and epigenetic modulation (Choi et al., 2015; Kamstra et al., 2018; Li et al., 2018), while neutron exposure in sea bass

embryos preserved gross developmental viability but induced detectable DNA-damage signatures (Przybyla et al., 2025). Early developmental success, therefore, does not preclude latent genomic instability or long-term performance consequences.

For translational reliability, factorial experimental designs that maintain separability between gravitational alteration and ionizing radiation exposure are indispensable (Proshchina et al., 2021). Without such separability, mechanistic attribution becomes conflated, and subsystem risk modeling loses analytical precision.

Methodological heterogeneity remains a structural limitation in the current evidence base. Ground-based analog systems differ in kinematic regimes and fluid dynamic artifacts (Hammond and Allen, 2011; Wuest et al., 2015; Brungs et al., 2016), whereas authentic in-flight platforms provide ecological validity but are constrained by duration, replication limits, and hardware restrictions. These streams of evidence are therefore stratified rather than interchangeable.

In aquatic systems, suppressed buoyancy alters gas–liquid mass transfer, oxygen distribution, carbon dioxide retention, and nitrogen species dynamics (Herranz et al., 2013; Fili et al., 2020; Poughon et al., 2020). Consequently, phenotypes observed under simulated microgravity may arise through distinct mechanistic pathways depending on shear profile, mixing architecture, and phase-separation efficiency. The absence of standardized aquatic-specific environmental reporting, including continuous dissolved oxygen monitoring, total ammonia nitrogen turnover kinetics, shear descriptors, and hydraulic residence time metrics, limits cross-study comparability. Extension of minimum reporting standards, including adaptation of the Bonn criteria to aquatic bioprocess variables (Hammond and Allen, 2011), would substantially enhance interpretive coherence.

Closed-loop aquatic architectures critically depend on microbial nitrification and biofilm stability for nitrogen management. Yet microbial community dynamics under altered gravity and radiation exposure remain incompletely characterized (Marra et al. 2023)). Altered convection may reshape oxygen gradients within biofilms, potentially influencing the stability of ammonia-oxidizing and nitrite-oxidizing populations. A subtle imbalance in nitrifiers could destabilize nitrogen cycling before overt organismal distress becomes evident. Microbial fragility, therefore, represents a plausible hidden limiting variable in extraterrestrial aquaculture systems.

Dormant-stage invertebrates, particularly *Artemia* cysts, demonstrate post-flight reactivation and survival (Novikova et al., 2011; Alekseev et al., 2022). While dormancy-based resilience supports logistical robustness, it does not resolve sustained protein productivity or trophic integration performance under continuous closed-loop operation.

Similarly, MELiSSA-associated photobioreactor developments and ISS-linked systems confirm oxygen production and carbon assimilation under microgravity conditions (Lasseur et al., 2010; Detrell, 2021; Fahrion et al., 2021). However, phase separation and gas transfer limitations under suppressed buoyancy emerge as dominant engineering constraints (Fili et al., 2020; Poughon et al., 2020). Across organism groups, system observability, environmental control precision, and failure-mode containment increasingly define performance boundaries.

The cumulative evidence supports reframing extraterrestrial aquaculture as a coupled organism-environment-hardware system operating under extraterrestrial boundary conditions. This

connectivity-oriented framework diverges from organism-centered exploratory biology by explicitly treating biological viability and environmental controllability as co-dependent variables within a single dynamic architecture. Feasibility must therefore be defined in terms of reproducible subsystem stability rather than isolated organismal tolerance.

Operationalization requires quantifiable performance descriptors. Mission-relevant metrics include nitrogen turnover resilience bands, dissolved oxygen fluctuation amplitude under altered convection, carbon dioxide retention dynamics, feed conversion ratio stability, skeletal mineral density trajectories across generations, and behavioral stability indices at realistic stocking densities. Without defined stability envelopes, mission readiness remains conceptually indeterminate.

This review is constrained by platform heterogeneity, short mission durations, a concentration of evidence in model organisms, incomplete reporting of environmental metadata, and limited multi-generational datasets. Chronic skeletal remodeling trajectories, epigenetic drift, and microbial community evolution under sustained altered gravity remain insufficiently quantified. (Salazar et al. 2023)

Advancement toward subsystem deplorability requires a staged validation pathway. Initial phases should isolate individual stressors through factorial gravity and radiation designs to establish mechanistic clarity. Subsequent phases must integrate organismal, microbial, and environmental subsystems within controlled closed-loop prototypes equipped with continuous monitoring. Long-duration, multi-generational assessments at realistic biomass densities are then required to evaluate chronic stability. Final validation demands flight testing under mission-representative timelines with embedded monitoring architectures and predefined failure-mode containment protocols.

Collectively, extraterrestrial aquaculture has established biological survivability across taxa. The next phase must establish stability, predictability, and controllability under mission-representative constraints. Only through quantified performance envelopes, structured risk taxonomy, and staged translational validation can the discipline advance from experimental resilience to operational legitimacy.

### *Species Proposed for Future Investigation*

**Table 1.** Candidate species proposed for space aquaculture research

<b>Organism group</b>	<b>Candidate species</b>	<b>Proposed functional role</b>	<b>Operational relevance</b>	<b>Evidence status within space relevant literature</b>
<b>Microalga</b>	<i>Tetraselmis suecica</i>	Oxygen generation and biomass production for feed integration  (Pérez-López et al., 2014)	High density cultivation potential and established use in feed chains make it a practical BLSS adjacent	Space relevant validation remains to be established and should be treated as pending systematic

			producer candidate	evidence mapping
<b>Microalga</b>	<i>Pavlova lutheri</i>	Biomass source for larval and formulated feeds; candidate phototrophic module  (Shah et al., 2013)	Favorable nutritional profile supports inclusion when feed value is an explicit selection criterion	Spaceflight or microgravity specific datasets appear limited and require confirmation through targeted literature review
<b>Macroalga</b>	<i>Gracilaria spp.</i>	Oxygen contribution, nutrient uptake, and biomass for feed supplementation  (Emam et al. 2025)	Enables evaluation of macroalgal stability and nutrient coupling within closed-loop aquatic systems	In orbit evidence remains uncertain and should be framed as requiring verification
<b>Macroalga</b>	<i>Ulva spp.</i>	Oxygen production, rapid biomass accumulation, nutrient capture, feed additive  (Hofmann et al., 2025)	Rapid growth and bioremediation capacity allow stress testing of system control and harvesting strategies	Operational performance under space relevant conditions requires confirmation; definitive claims should be avoided without sources
<b>Aquatic plant</b>	<i>Wolffia spp.</i>	High protein biomass production with auxiliary oxygen contribution in minimal volume  (Pagliuso et al., 2022)	Extremely small morphology combined with high productivity supports its evaluation as a volume efficient feed node	Some Lemnaceae related taxa may have space associated reports; verification is required at

				genus and species level
<b>Demersal fish</b>	<i>Solea solea</i>	Edible protein source; operationally relevant fish candidate  (Imsland et al. 2011)	Demersal behavior facilitates assessment of feeding efficiency, welfare indicators, and collision risk in confined systems	Spaceflight evidence is likely sparse and the species should be framed as an operationally motivated candidate
<b>Demersal fish</b>	<i>Scophthalmus maximus</i>	Edible protein source; high-value aquaculture species  (Bjørndal and Øiestad, 2011)	Strong terrestrial aquaculture relevance for testing density tolerance, growth performance, and waste loading in RAS like systems	The existence of altered-gravity studies should be verified; otherwise justification should rely on terrestrial RAS evidence
<b>Demersal fish</b>	<i>Paralichthys olivaceus</i>	Edible protein source; demersal operational model species  (Stieglitz et al. 2011)	Provides a bridge between mechanistic vertebrate models and aquaculture grade operational constraints	Space specific datasets may be absent and the species should be positioned as a bridge candidate for future subsystem trials
<b>Demersal fish</b>	<i>Gadus morhua</i>	Edible protein source with high metabolic and waste output demands  (Puvanendran et al., 2022)	Effectively stress tests water chemistry regulation, microbial control, and feeding stability under constrained conditions	Requires cautious framing; coldwater RAS evidence is informative but does not constitute space relevant validation

<b>Demersal fish</b>	<i>Pleuronectes platessa</i>	Edible protein source; demersal behavior and welfare assessment candidate  (Kendler et al., 2024)	Supports analysis of welfare, behavioral stability, and system and organism coupling under confinement	The extent of any microgravity or analog evidence should be verified; otherwise, the species should be justified on operational grounds
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## Conclusion

This study synthesized the scope of extraterrestrial aquaculture (space aquaculture) by summarizing the principal organism groups investigated to date and the core system architectures in which they have been tested. Across the compiled literature, the necessity of examining aquatic organism metabolism and performance under space relevant physical constraints is clear, particularly under radiation exposure and altered gravitational acceleration regimes such as microgravity. The evidence supports the view that space aquaculture is not merely “aquatic biology in space,” but a coupled problem in which organismal responses, hardware design, and operational constraints interact to shape outcomes. In this sense, the field embodies connectivity as a scientific principle; seemingly separate systems, including fluid physics, gas handling, microbial dynamics, life support control, and organism physiology, function as an integrated network rather than independent layers. By framing the evidence within this coupled systems perspective, this review helps reduce a key gap in the literature, namely the lack of an integrative synthesis that connects biological findings to subsystem level implications.

At the same time, the high cost of space missions and the limited number of long-duration experiments indicate that humanity remains at an early stage in developing reliable aquatic production beyond Earth. Current results are strongest at the proof of feasibility level and for short to mid-duration demonstrations, while the operational maturity required for sustained, maintenance-bounded production in closed loop habitats is not yet consistently demonstrated. The path forward, therefore, requires a deliberate shift toward standardized reporting, comparable performance metrics, and experiments designed around operational scenarios rather than survivability alone. On the other hand, this synthesis illustrates that research areas often treated as conceptually unrelated, space sciences on the one hand and terrestrial aquaculture on the other, are in fact evaluated through a common systems-based framework, in which constraints, feedback mechanisms, and performance limits remain comparable across environments.

From this standpoint, the literature further indicates that future in situ investigations cannot rely solely on biological experimentation but must be developed in coordination with supporting disciplines, including astrohydrogeology, in which fluid occurrence, transport processes, and geochemical stability directly shape the viability of closed aquatic systems beyond Earth.

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### Ethical approval

### Informed consent

Not available.

### Data availability statement

The authors declare that data can be provided by the corresponding author upon reasonable request.

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There is no conflict of interests for publishing this study.

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### Contribution of authors

Conceptualization, A.B.M. and A.T.; methodology, A.B.M. with guidance from A.T.; literature search and screening, A.B.M.; synthesis and interpretation, A.B.M. and A.T.; giving hypothesis, and suggestions; writing, original draft, A.B.M.; final editing, A.B.M. and A.T.; supervision, and article administration; final review A.T. All authors have read and agreed to the published version of the manuscript.

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