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Review

The Ohrid Trout: A "Living Fossil" Endemic to Lake Ohrid Left Behind by Science

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Abstract

The Ohrid trout (*Salmo letnica*) is a species endemic to Lake Ohrid (shared by Albania and North Macedonia), which is internationally recognized for its geological longevity and unique natural features. Given that the species has distinctive biological, ecological, and evolutionary characteristics, as well as significant economic value, the decline in this trout's population is a serious and urgent problem, deserving continuous, scientifically based management. Yet, although it is considered a "Fossil Trout", research on this species remains limited in relation to science and conservation. To understand the current state of the art, we conducted a systematic review in Web of Science, analyzing 31 indexed articles about the Ohrid trout. These studies primarily focused on the seasonal morphological characteristics of specific organs, phylogenetics, and, to a lesser extent, the impacts of environmental contamination. However, notable gaps exist in understanding sex- and stage-specific physiology, morphotype diversity, and pollutant bioaccumulation. To address these limitations, integrative strategies that combine multi-omics biomarker development, genetic screening of broodstock, and systematic monitoring of pollution and climate-related stressors are crucial. Regional authorities should work with international organizations to establish long-term monitoring of *S. letnica*. This review aims to provide a critical foundation for overcoming the "Living Fossil Left Behind by Science" paradigm and to foster global initiatives to preserve the long-term survival and evolutionary legacy of this endangered species.

Keywords: *Salmo letnica*; endangered species; relic species; conservation

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1. Introduction

Located between the Republics of Albania and North Macedonia, Ohrid Lake is one of Europe's and the world's oldest lakes, estimated to be at least two to five million years old. It is also one of the deepest, reaching a maximum depth of 293 m [1], with a total area of 358 km^2 [2,3]. Such notable depth, combined with a low influx of sediments, has ensured the existence of today's Lake Ohrid, as lakes often become filled with sediment after approximately 100,000 years. UNESCO first listed the Ohrid Lake region on the World Heritage List in 1979 under natural criteria, and one year later, it was added as a natural and cultural property [4]. The lake is often referred to internationally as a "Museum of

Living Fossils", owing to its high biodiversity of unique species (more than 200), ranging from phytoplankton to predatory fish [2]. Between 1930 and 1957, Ohrid Lake was also known as "Trout Lake"; however, the most abundant species is actually the common carp (*Cyprinus carpio*) [5]. On top of the 10 endemic fishes, the most renowned is the Ohrid Lake trout (*Salmo letnica* Karaman, 1924) (Figure 1), with four morphotypes [6]. According to the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, *S. letnica* was classified as "endangered" on 22 March 2024 [7].

Figure 1. Representative adult female Ohrid trout (*Salmo letnica*) collected from Lake Ohrid at Peštani, North Macedonia, in January 2000. The 4+-year-old specimen (total length: 40 cm) was used for organ necropsy and scientific analysis.

Throughout the 20th century, this species experienced a continuous decline, characterized by dramatic decreases in total catches (including the size of the caught fish), the number of animals returning to spawning areas, the predominance of younger fish, and gender imbalances [8]. In 2003, the so-called "Fossil Trout" drew global attention and raised concerns about its rapid potential extinction in the Balkans [9,10]. Conservation efforts included a bilateral (Albania and Macedonia) restocking program aimed at restoring Ohrid Lake's trout population [11]. Despite that, significant threats to Lake Ohrid continue to jeopardize the survival of *S. letnica* (Figure 2). Moreover, the introduction of Ohrid trout into Serbian lakes has highlighted its potential to act as an invasive species outside its native territory, threatening the local trout biodiversity [12].

Significant investments, such as the World Bank's 1998 funding of the Lake Ohrid Conservation Project—Global Environment Facility Trust Fund Grant Agreement [13], established the foundation for the region's management and conservation. Even local populations in the Republic of Macedonia and Albania recognized the economic importance of the Ohrid trout and expressed willingness to contribute financially to its protection [14]. In fact, Ohrid trout has been reared in aquaculture mainly for restocking but also for human consumption [15]. Despite these efforts, the species' limited distribution, unique evolutionary history, and ongoing population decline mean that the Ohrid Lake trout remains surprisingly understudied and largely overlooked in the international scientific community.

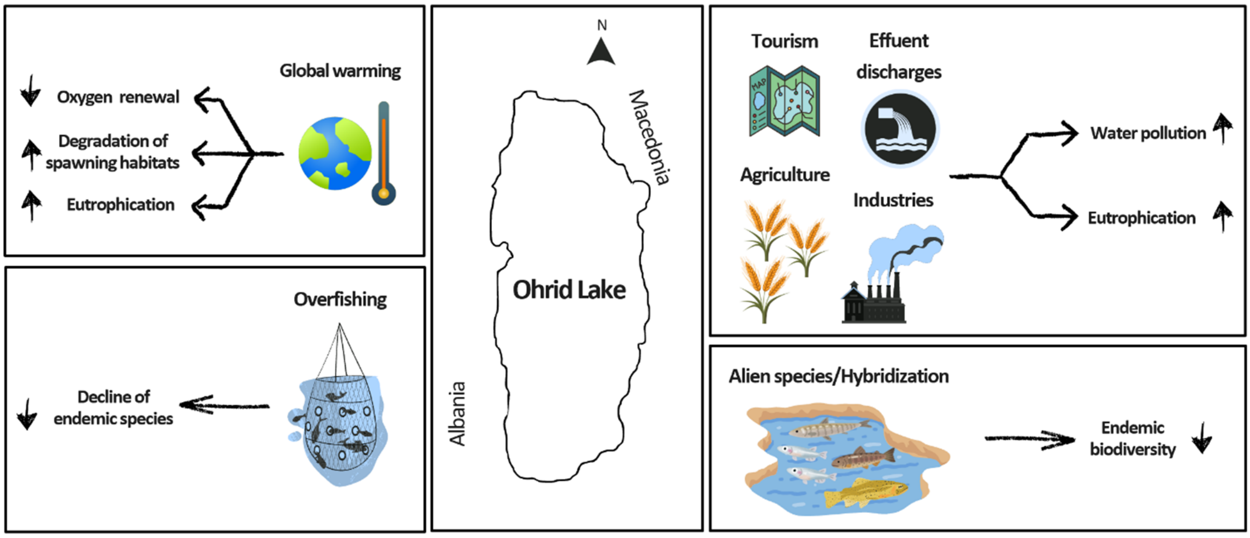

Figure 2. Main risks to the sustainability of Ohrid Trout.

2. Methodology

To investigate this caveat from both quantitatively and qualitatively perspectives, a systematic search was conducted using Clarivate's Web of Science platform, a highly respected and arguably the most influential bibliographic data source worldwide [16]. The search was made on the 18th of September 2025 using the keywords "*Salmo letnica*" or "Ohrid trout" or "Ohrid Lake trout". This search resulted in 34 indexed articles focused on the species' biology (23.5%), environmental science (20.1%, including pollutant effects such as metals), and anatomical morphology (14.7%), especially of the liver. The initial set was refined by excluding studies that only mentioned the species in their references. Ultimately, 31 articles were included (listed in Table S1 and Figure S1) and used to summarize the main topics of the current state of knowledge on *S. letnica*.

All studies published in non-English journals or in non-peer-reviewed or non-indexed sources were excluded a priori, since such publications are not readily available to most international researchers or through scientific databases.

3. Results and Discussion

3.1. Seasonal Organ-Specific Changes

The liver is the most extensively investigated organ in Ohrid trout, both in terms of structure and function. A seasonal study revealed that the hepatosomatic index (HSI) reached its peak during late vitellogenesis, resulting from increases in both hepatic parenchyma and stroma. Parallel to this, the gonadosomatic index (GSI) also peaked during late vitellogenesis and spawning, correlating with plasma 17β-estradiol (E2) levels [17]. The characterization of hepatocyte ultrastructure in terms of lipid, glycogen, rough endoplasmic reticulum (RER) content [18], dense bodies, and crystalline inclusions [19] in female Ohrid trout revealed a seasonal and species-specific pattern when compared to other trout species. Lipids emerged as the main building blocks to support female reproduction, with higher levels during the onset and mid-vitellogenesis stages [18].

The pigment content of liver macrophages in this trout was also reported to be distinctive of this species [20]. These cell aggregates primarily contained hemosiderin and/or lipofuscin, rather than melanin, which may be related to habitat-specific factors. Additionally, the liver macrophage aggregates exhibited seasonal variation, with higher relative and total volumes in relation to the liver, parenchyma, and stroma being found during the post-spawning reproductive phase of intense hepatocyte remodeling [20]. A similar increase was observed in hepatic rodlet cells during spawning and post-spawning [21].

In a series of morpho-functional seasonal studies, the same authors evaluated the presence of macrophage aggregates in different portions of the kidneys of adult female Ohrid trout [22]. In this organ, the obtained profile was distinct from what they observed in the liver—the kidney macrophages aggregates peaked at late vitellogenesis and decreased in the post-spawning stage. Pigment aggregate composition was also organ-specific, as the kidney showed melanin abundance [22]. The Ohrid trout spleen analysis during spawning showed distinct pulp separation, with red pulp volume decreasing and white pulp volume increasing compared to early–late vitellogenesis [23].

Overall, evidence from various morphological studies on Ohrid trout suggests that the seasonal dynamics observed in the liver, kidney, and spleen are closely connected to fluctuations in sex steroid hormones. These cited studies provide a strong foundation for future histopathological research on biotic or abiotic factors that trigger physiological adaptation or cause lesions.

3.2. Biodiversity and Conservation

The Ohrid trout is said to have four distinct morphotypes (*typicus*, *aestivalis*, *balcanicus*, and *lumi*), which differ in their morphological characteristics, spawning seasons and ecological preferences [6,8,24]. The external features of Ohrid trout have been described, highlighting sex-dimorphic characteristics related to body color, head shape, scales, spot distribution, and pigmentation [24]. Among the morphotypes, the *S. letnica lumi* is long, with a robust body and consistently exhibiting black spots on the head and operculum [24]. *S. letnica lumi* spawns in small tributaries and is very difficult to catch in Ohrid Lake [25]. Further, the *S. letnica typicus* predominantly spawns in winter (January–March), whereas *S. letnica aestivalis* is a summer spawner (July–August) [8]. Morphotypes also have distinct spawning locations along Ohrid Lake and substrate preferences ranging from rocky bottoms (e.g., *S. letnica aestivalis*) to fine sand (e.g., *S. letnica balcanicus*) [8].

This ecological complexity underscores the importance of targeted management efforts. Therefore, for the conservation of *S. letnica*, management actions should ensure the protection of its distinct ecological forms, spawning habitats, and reproductive seasonality. The importance of studying *S. letnica*, its phylogeny, and its morphotypes has been recognized, but current data on this topic remain limited [25]. There is evidence of minimal mitochondrial genetic differentiation, suggesting ecological divergence without fixed mitochondrial separation [25]. Further, data also suggest that *S. letnica typicus* and *S. letnica aestivalis* originated sympatrically within Lake Ohrid [26]. Additional genetic analyses are needed to clarify the taxonomic status of the different morphotypes.

Phylogenetic trees based on mitochondrial sequences have disclosed the relationship between *S. letnica* and other *Salmo* species in Lake Ohrid [27]. It is genetically distinct from other Adriatic populations but is likely derived from the Adriatic brown trout (*Salmo trutta*) lineage [28,29]. Specifically, Talarico et al. (2024) studied the diversity of class II Major Histocompatibility Complex (MHC-DAB) genes in Ohrid trout. Given the central role of MHC in antigen recognition and pathogen-mediated immune defense, the discovery of high and novel MHC-DAB variation, with limited overlap with other trout species, suggests strong population-specific immune adaptation, which is essential for the conservation of this species [30]. Other genetic analyses, including mitochondrial DNA control region and microsatellites, confirmed that *S. letnica* is distinct from *S. ohridanus*, despite both species inhabiting Lake Ohrid. *S. ohridanus* represents an ancient member of the genus *Salmo*, which diverged from the common ancestor of the *S. trutta* complex more than four million years ago [28]. This species is closely related to the Adriatic lineage of *Salmo obtusirostris* [28,31]. *S. letnica* and *S. ohridanus* have distinct morphology, namely in terms of the body shape, the latter being presumably more elongated due to its preference for deeper lake zones [28]. Ecological niche differentiation probably limited competition and promoted their sympatric persistence in Lake Ohrid. Additionally, the presence of limited hybridization reinforces the existence of reproductive intralacustrine isolation between these taxa [28].

3.3. Environmental Pollution and Fish Health

Only a few surveys have investigated parasitic and viral infections in Ohrid trout over the years. In the study of Stojanovski et al. (1998), parasitic infections were present in 76% of the examined fish, by six parasite species (*Diclybothrium* sp., *Eubothrium crassum*, *Eubothrium salvelini*, *Cyathocephalus truncatus*, *Proteocephalus neglectus*, and *Pomphorhynchus* laevis) [32]. Additionally, infectious hematopoietic necrosis virus (IHNV) was found in 33.3% of the samples, indicating significant health risks for this species [33]. A diversity of liver lesions was described in adult female Ohrid trout captured in two urbanized areas of Lake Ohrid, including lymphocytic infiltration, necrosis, cholangiofibrosis, bile duct hyperplasia, and parasites within bile ducts. Although liver lesions were common in trout from the urbanized sites (affecting 40% and 27% of the fish), they were rare at the reference site (only 7% of the fish) [34]. To assess the fitness of Ohrid trout, researchers used statistical methods and support vector machine models to analyze their growth dynamics in both experimental and natural environments [35].

Regarding environmental pollution in Ohrid trout, a study that quantified heavy metal levels in distinct ecosystem compartments (water, sediments, and biota) of Lake Ohrid found that sediments and plants were the most contaminated, while metals were not detected in Ohrid trout gills, liver, and muscle [36]. Despite this, other studies showed that certain metals, specifically copper and iron, accumulated. These metal profiles varied across the various phases of the reproductive cycle of female Ohrid trout, with the highest loads observed in the post-spawning phase [37]. Furthermore, recent research has documented seasonal buildup of toxic metals in Ohrid trout tissues, with metal levels in muscle generally remaining below food safety limits [38], although cadmium levels exceeded the admissible thresholds [39].

4. Current Gaps and Strategies for Protecting Ohrid Trout

Given the unique biological and ecological characteristics of the Ohrid trout, as well as its IUCN-listed endangered status, the conservation of this species should be regarded as an international priority, requiring integrative research, regulatory frameworks, and funding support, along with the active participation of local communities. Accordingly, as the study and conservation of this trout species represents a global concern and challenge, the validation and dissemination of information should occur on an international scale rather than remain confined to local or regional contexts. Although various protective measures, such as fishing regulations, have been implemented over the years [40], this systematic review highlights a significant lack of Web of Science-indexed studies and identifies critical knowledge gaps that can serve as starting points for future conservation strategies. The most urgent gaps fall into three main areas, as outlined below.

4.1. Physiological and Omics Screening

Specific histomorphological features of Ohrid trout include the predominant lipid accumulation during vitellogenesis [18], the distinct pigment composition of hepatic macrophages [20], and the seasonal changes in pigmented macrophages within the liver [20] and kidney [22] across the reproductive cycle. In this context, integrating lipidomic, transcriptomic, and proteomic approaches could enable the identification of key molecular pathways and regulatory mechanisms, linking morpho-physiological data, gene expression patterns, and metabolic dynamics.

Such multi-omics strategies are crucial for developing reliable species-specific biomarker panels that support long-term biomonitoring and conservation efforts. These biomarkers would facilitate, for instance, the accurate discrimination of reproductive stages by improving the efficiency of artificial breeding and restocking programs. It is essential to note that all seasonal histomorphological studies conducted to date have focused solely on adult females, primarily examining the liver, spleen, and kidneys. Future research should include adult males and immature individuals to determine whether these markers show sex- and stage-specific variations. Lastly, applying these biomarker-based approaches in comparative studies with other trout species would provide a broader understanding of evolution, highlighting adaptive features of *S. letnica*. In view of the endangered status of the species, prioritizing minimally invasive sampling techniques (e.g., blood, mucus, scales, tissue biopsies) should be a primary focus [41].

4.2. Managing and Restocking

Restocking programs have been implemented to support the maintenance of Ohrid trout populations in Lake Ohrid [11]. Stocking activities involving fingerlings and/or alevins produced at the fish breeding stations in Ohrid (Macedonia) and Lin (Albania) have been implemented for several decades [40]. Despite that, studies indicate a population decline and a predominance of specific morphotypes over others [25]. In fact, artificial fertilization has mainly relied on *S. letnica typicus*, a practice that likely disrupts the natural genetic and ecological balance within *S. letnica* populations. In this context, rare morphotypes (*S. letnica lumi*) should be given special attention in conservation efforts. To avoid the loss of morphotype diversity and the risk of genetic population homogenization, it is essential to conduct integrative genetic and physiological screenings of broodstock and restocked individuals. This approach would help preserve the evolutionary heritage of *S. letnica* and enhance the species' resilience against threats, such as overfishing, aquatic pollution, and climate change, particularly warming. In addition, launching a pilot-scale tagging program in restocking Ohrid trout could be a valuable way to assess the ecological specificities of the morphotypes and the restocking efficiency [42]. Using molecular tools, like environmental DNA (eDNA), which is cost-effective and sensitive for detecting fish presence and estimating abundance [43], alongside acoustic-optical surveys, which are especially useful in large or deep-water bodies [44], would be highly valuable for assessing and monitoring population abundance and biomass.

4.3. Monitoring Contaminants and Climate Change Impacts

A key priority is the establishment of systematic monitoring programs to assess both the current and the future contamination status of Lake Ohrid and the bioaccumulation potential in Ohrid trout tissues. To date, only a limited number of studies have addressed this issue, focusing on heavy metals [38] and pesticides [45]. There is a lack of information on the presence, environmental distribution, and bioaccumulation of pharmaceuticals, which are internationally considered as priority emerging contaminants in aquatic ecosystems [46].

Furthermore, ongoing climate change poses further challenges. Rising global temperatures have a direct impact on aquatic environments, with freshwater systems, such as lakes, being particularly vulnerable [47]. Warming leads to well-documented alterations in lake dynamics, including changes in water column mixing, water levels, and lower dissolved oxygen concentrations [47,48]. As a cold-adapted species, Ohrid trout is likely to alter its spatial distribution, seeking thermally suitable refuges during warmer months.

Being a salmonid, the Ohrid trout may also exhibit changes in growth rate, behavior, and reproductive patterns in response to thermal stress [49]. Therefore, the Ohrid trout population's sustainability will depend on proactive management, including the protection of cold-water niches, conservation of spawning areas, and reduction in anthropogenic contamination. Implementing biomonitoring programs that combine contaminant assessment with climate-related stressors is therefore urgent, as these tools can guide adaptive management strategies aimed at reducing the impacts of warming and heatwaves and ensuring the long-term survival of Ohrid trout.

5. Conclusions

Ohrid trout is a particularly attractive species, not only for its endemism but also for its evolutionary significance. Yet, only 31 articles indexed in the Web of Science address aspects like morphological seasonality, phylogenetics, and environmental impacts. Major knowledge gaps persist regarding sex- and stage-specific physiology, morphotype diversity, and pollutant bioaccumulation. Filling these gaps is essential for a comprehensive understanding of the species' biology and for guiding effective conservation and management strategies for *S. letnica* in Lake Ohrid. Specific monitoring metrics, such as recapture data from tagged individuals and assessments of genetic diversity, will be crucial for achieving this goal. Conservation efforts should prioritize the protection of wild populations. This can only be ensured through strong local engagement and coordinated international collaboration.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/hydrobiology4040032/s1, Figure S1: Distribution of the number of indexed articles in Clarivate's Web of Science over the years; Table S1: List of the 31 articles focusing on Ohrid Trout, retrieved from Clarivate's Web of Science.

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