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Spatial Distribution Pattern and Influencing Factors of Petromyzontiformes Worldwide

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Abstract. As the most primitive extant jawless vertebrates, Petromyzontiformes have an evolutionary history dating back hundreds of millions of years, with approximately 50 known extant species globally, mainly distributed in temperate and frigid waters across all continents except Africa. They hold irreplaceable value as model organisms in vertebrate evolution research due to their unique biological characteristics such as the origin of the "new head" structure and central nervous system regeneration ability. Petromyzontiformes are highly sensitive to environmental changes, and their migratory behavior and population dynamics are jointly affected by ecological factors and human activities. In this study, we analyzed the global spatial distribution pattern of Petromyzontiformes, which presents a distinct antitropical distribution feature, concentrated in the temperate zones of the Northern Hemisphere and the mid-to-high latitudes of the Southern Hemisphere. We further explored the key environmental factors restricting their distribution, including water temperature, water quality, flow velocity, substrate type and salinity, among which low tolerance to high water temperature is the primary factor restricting their expansion into tropical regions. In recent decades, human activities such as habitat fragmentation, water pollution, overfishing and climate change have severely threatened the survival of Petromyzontiformes populations, leading to the contraction of distribution ranges and even local extinction risks for some species, while a few species have caused serious ecological damage as invasive species. This study also summarized the current research methods for Petromyzontiformes distribution, including field sampling, environmental DNA technology and species distribution models, and highlighted key research gaps such as the lack of multi-factor interaction analysis and long-term monitoring data. Finally, we proposed future research directions and conservation strategies, aiming to provide scientific basis for the protection, habitat management and restoration of Petromyzontiformes, and to safeguard the biodiversity and evolutionary research value of this ancient vertebrate group.

Keywords: Petromyzontiformes, Distribution, Water quality

1. Introduction

Petromyzontiformes, as the most primitive extant jawless vertebrates, trace their evolutionary history back hundreds of millions of years [1]. At present, there are about 50 known extant species worldwide, mainly distributed in temperate and frigid waters on all continents except Africa. In the

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biological field, lampreys have attracted extensive attention due to the origin of their unique "new head" structure and the regenerative capacity of the central nervous system, and hold an irreplaceable value as model organisms in vertebrate evolution research [2,3]. Lampreys are particularly sensitive to environmental changes and are affected by a variety of endogenous and exogenous factors. On the one hand, anadromous migration is an essential component of the life cycle of some species, involving complex physiological adaptations and behavioral patterns. It typically includes the metamorphosis from freshwater benthic filter-feeding larvae to parasitic larvae, followed by migration to seawater (or large freshwater water bodies for landlocked populations), and finally, adult individuals return to rivers and spawn in freshwater [4]. This migratory behavior enables lampreys to cope with the challenges of different aquatic environments and supports their growth, reproduction and species continuation. On the other hand, the abundance and distribution of lampreys are subject to the combined impacts of climate change, pollution, overfishing and other human activities, which may force lampreys to migrate to higher latitudes or altitudes or even face extinction. For example, the sea lamprey (Petromyzon marinus), native to the Atlantic Ocean, was introduced into the North American Great Lakes region in the early 20th century, causing severe damage to local fisheries [5]. By the end of the 21st century, the sea lamprey populations in southwestern Europe may face the risk of local extinction, leading to a continuous decline in biodiversity [6]. Given their unique value as model organisms and the survival threats posed by environmental changes, the conservation of lampreys is extremely urgent. Therefore, this study intends to explore the distribution pattern of lampreys and their correlations with environmental factors by analyzing key environmental indicators, aiming to reveal the main driving factors affecting the survival and spatial distribution of their populations. In doing so, we hope to provide a scientific basis and theoretical support for formulating targeted conservation strategies and optimizing habitat management and restoration measures.

2. Research progress

A bibliometric analysis of literature on Petromyzontiformes published from 1981 to 2025 was conducted based on the Web of Science database. This analysis reveals the development dynamics of this research field and the global distribution of scientific research forces from two dimensions: the trend of literature output and the contributions of countries/regions.

2.1. Annual analysis

The annual number of published papers on lamprey research shows a distinct phased growth characteristic (Figure 1). From 1981 to 2007, the annual number of papers remained relatively stable, fluctuating between 24 and 66 with an average of about 42 papers per year, indicating that the research was in a stage of steady accumulation during this period. Since 2008, the literature output has increased significantly, with a peak appearing especially between 2014 and 2017 (88 papers in 2014 and 100 papers in 2016), and reaching the highest point to date in 2021 (142 papers). This period of rapid growth may be related to the popularization of next-generation genome sequencing technology, the rise of evolutionary developmental biology (Evo-Devo), and the increasingly prominent status of lampreys as model organisms at the key node of vertebrate evolution. The number of published papers has declined since 2022 but remains significantly higher than the early level, suggesting that the field may be undergoing a phase of consolidation or the emergence of new research frontiers. Overall, the literature output in this field over the past 45 years has shown a trend of "steady accumulation - rapid growth - high-level adjustment", reflecting that lamprey research has gradually developed from a relatively niche field of traditional taxonomy and morphology to an active interdisciplinary field integrating modern molecular biology and genomics [7].

2.2. National and regional distribution

An analysis of the proportion of papers published by different countries and regions shows that global lamprey research presents a pattern of high concentration and multi-polar cooperation (Figure 2). The top ten countries/regions contribute a cumulative 74.408% of the total literature. Among them, the United States ranks first with an absolute advantage of 39.549% of the total literature, being the leading force in this field, which is closely related to its overall scientific research strength in the life sciences, financial investment, and advantageous resources of having multiple lamprey model species. Canada (15.39%) and Japan (9.807%) rank second and third respectively; they are either the original distribution areas of important lamprey species or have traditional advantages in neurobiology and genomics research of lampreys. European countries such as Sweden (8.697%) and England (5.154%) also make significant contributions, reflecting Europe's profound accumulation in evolutionary biology and comparative physiology. The above results indicate that the core scientific research output is concentrated in a small number of developed countries and China. Other countries account for a considerable proportion (25.592%), suggesting that lamprey research has a certain universality on a global scale.

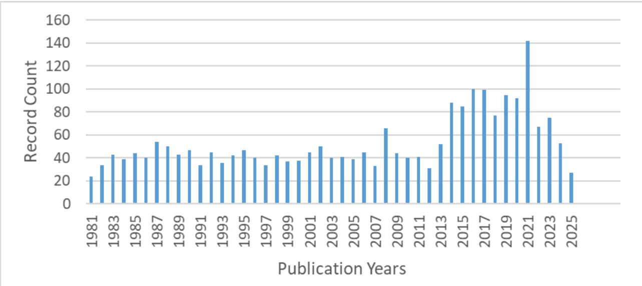

Figure 1. Annual publication trend

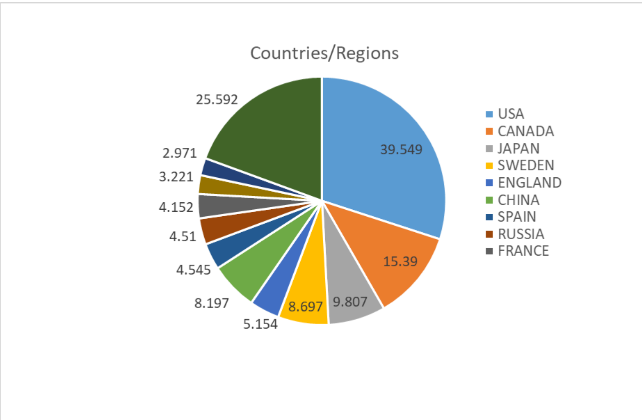

Figure 2. Main countries of literature publication

DOI: 10.54254/2753-8818/2026.BH32162

3. Research content

3.1. Spatial distribution

The global distribution of lampreys presents a distinct antitropical distribution pattern, i.e., they are mainly distributed in the temperate zones of the Northern Hemisphere and the mid-to-high latitudes of the Southern Hemisphere, which can be divided into three main regions, with almost no records in the equatorial region (Figure 3). The Northern Hemisphere distribution area is the center of species diversity. Among them, Petromyzoninae is distributed only in the Northern Hemisphere, with the two sides of the North Atlantic (from Norway to Morocco, and from the St. Lawrence River in North America to Florida) and the northern part of Eurasia as the main distribution areas. Petromyzon marinus, the only species of the genus Petromyzon, is widely distributed in the coastal waters of the United States, Canada, Iceland and Europe, while the genus Caspiomyzon is found only in the Caspian Sea basin. The Northeast Asian region is concentrated with a number of endemic species: Lethenteron reissneri mainly inhabits the freshwater environments of northeastern China, northern Japan, northern Korea and the Russian Far East, and does not migrate throughout its life; Lampetra japonica and Lampetra morii are found in the Amur River, Tumen River basin and Yalu River basin of China respectively, with the former having both anadromous migratory habits and the latter being a small freshwater resident species. There are 3 species of lampreys in China, mainly inhabiting the northeast water systems such as the Amur River, Songhua River and Nenjiang River, among which Lethenteron reissneri is also recorded in the Ussuri River, Mudan River, Xingkai Lake and other waters. The distribution of lampreys in the Southern Hemisphere is relatively limited, mainly occupied by Geotriinae. For example, Geotria australis is distributed in the coastal waters of southern Australia, New Zealand and Chile, showing typical transoceanic anadromous migratory habits. The three species of the genus Mordacia inhabit the freshwater and coastal waters of southeastern Australia, Tasmania and Chile.

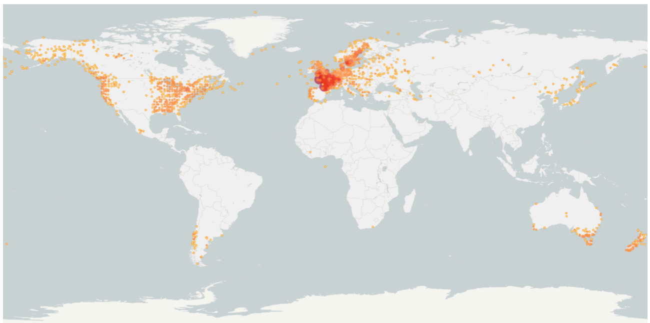

Figure 3. Global distribution of petromyzontiformes, data source: https://www.gbif.org

3.2. Influencing factors

The distribution of lampreys strictly depends on specific ecological conditions, and their habitats can be divided into two types: anadromous and freshwater resident. The habitat preferences of adult lampreys depend on their life history strategies. The vast majority of species are anadromous, which need to migrate between the ocean and freshwater, while non-parasitic or landlocked species live entirely in freshwater environments. For example, Lampetra japonica completes larval development in freshwater, then migrates to the ocean for a parasitic life, and swims upstream to spawn after sexual maturity; such species have a wide tolerance to salinity, surviving in freshwater (0 PSU) to

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offshore seawater (35 PSU), but their spawning grounds must meet the conditions of gravel substrate (2-5 cm in diameter) and dissolved oxygen > 6 mg/L [8]. Freshwater resident species, as reported by Yang et al [8], inhabit specific freshwater environments throughout their lives. Lampetra morii and Lethenteron reissneri in northeastern China belong to this category, mainly living in mountain rivers with microcurrent and sandy substrate. The larvae feed on filter-feeding plankton, and enter the reproductive period directly after metamorphosis without a parasitic nutritional stage. Water temperature and physiological tolerance are the most critical limiting factors determining the geographical distribution boundary of lampreys. Lamprey larvae (ammocoete) have extremely low tolerance to high water temperature, and this physiological characteristic restricts their spread to tropical waters, making it an important ecological threshold for their distribution boundary. At the same time, studies have shown that although a small number of species are distributed in high-altitude areas such as the Mexican Plateau, they generally conform to the biogeographic pattern of "being sensitive to heat but tolerant to cold" [9]. Global warming caused by climate change is expected to have an impact on the physiology, behavior and population dynamics of lampreys, which may lead to the contraction of their distribution range. Water quality conditions have a significant impact on the distribution of lampreys, among which flow velocity is an important indicator for lampreys to select habitats. Wu et al [10] conducted a quantitative analysis of the fish community diversity and habitat suitability in the Huntai River, and found that the optimal flow velocity for Lampetra morii is 0.59 m/s. In large dam-free river systems, the spawning sites of sea lampreys significantly overlap with high bottom flow velocity areas (0.5-1.5 m/s), and it has been confirmed that there is a water temperature-dependent selection behavior of low flow velocity refuges. In addition, dissolved oxygen (DO) is a key survival indicator. Studies have shown that lampreys have high requirements for dissolved oxygen, with DO > 6.0 mg/L required for artificial breeding and natural habitats, and the pH value maintained at 7.0-8.0 [11]. Lampreys are in a natural state when dissolved oxygen is sufficient (> 3.0 mg/L), and exhibit symptoms such as increased ventilation rate and agitation as dissolved oxygen declines. Lamprey larvae are usually buried in the substrate composed of fine sediments and organic matter, so substrate conditions are crucial for habitat selection. For example, lampreys in the spawning period prefer shallow water areas with fast flow velocity (0.5-1.5 m/s) and gravel substrate (2-5 cm in diameter) for nest building and spawning [12]. In addition to the above main influencing factors, salinity is also an important ecological factor. For anadromous species, the salinity gradient is an important navigation clue, and they can acutely perceive changes in salinity to locate estuaries and complete osmotic pressure regulation. Over the past century, human activities have become the dominant driving force changing the distribution pattern of lampreys. In Europe, lamprey populations in river basins such as the Rhine and Vistula are on the verge of extinction due to the blocking of migratory channels by dam construction, coupled with the silting of spawning grounds and the decrease in oxygen content caused by water pollution, and are currently listed in the protection list of the Bern Convention [13]. On the contrary, after the sea lamprey invaded the North American Great Lakes through artificial canals, its population broke out due to the lack of natural predators, resulting in a 99% reduction in native fish such as lake trout from 1920 to 1950, which has become a typical case of ecological invasion [5]. Habitat fragmentation is one of the main reasons for the decline of lamprey populations: dam construction blocks the migratory channels of lampreys. Due to the weak swimming ability of lampreys and the lack of jumping ability of bony fish, traditional dam designs often form insurmountable barriers. Physical obstacles such as dams will seriously hinder the migration of lampreys, leading to a decline in their population size. For example, on the Iberian Peninsula, dams have caused a 69-96% contraction of the sea lamprey's distribution range [6].

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4. Research methods

Current research on the abundance and distribution of lampreys mainly includes field sampling and model prediction. For benthic larvae, the traditional electric fishing method has instantaneity but is easily disturbed by water flow and difficult to cover the entire cross-section; to this end, researchers have developed improved benthic samplers (such as a rectangular trawl-type dredge), which can collect standardized sediment samples of a fixed area on soft substrates, significantly improving the detection rate and spatial representativeness of larvae per unit volume [14]. For adult individuals, the research relies on physical barrier devices (such as fish ladders and trapping weirs) combined with manual counting or video monitoring systems, the effectiveness of which depends on the placement aligning with hydrological rhythms. For example, when the water temperature rises to 10–15℃ and the flow reaches the threshold in spring, setting traps upstream of the confluence of tributaries can capture more than 85% of migrating individuals [15]. Although such methods provide original count data, they have serious sampling biases. Environmental DNA (eDNA) technology is rapidly becoming a disruptive tool to break through the bottleneck of traditional sampling. Its principle is to enrich and amplify lamprey-specific mitochondrial gene fragments (such as 16S rRNA) from water bodies, realize absolute quantification of trace DNA through digital PCR or high-throughput sequencing, and overcome the difficulties of morphological identification [16]. However, this method is affected by hydrological, microbial and other conditions, with certain errors. In addition, on-site species monitoring usually adopts sample point or quadrat monitoring, resulting in difficulties in judging and obtaining data in unmonitored areas of species. To ensure the authenticity and integrity of species distribution, models can be established based on existing species occurrence data for simulation or prediction, thus promoting the development of research related to Species Distribution Models (SDMs). Species distribution models establish the correlation between species occurrence points and environmental factors to predict the potential distribution areas of species under current or future environmental conditions, which provides direct support for practical conservation issues such as endangered population identification, habitat restoration assessment, climate change response prediction and invasion risk management [17].

5. Research limitations

The current research on lamprey distribution has the following deficiencies. First, there is a lack of research on multi-factor interactions. Existing studies mostly focus on single-factor analysis (such as only considering water temperature or flow velocity), and lack systematic analysis of the interactions of two or more factors. For example, key mechanisms such as the synergistic effect of water temperature and flow velocity, and the spatial coupling relationship between substrate type and water depth have not been fully explained. This research gap makes it difficult to accurately predict the distribution response of lampreys under complex environmental gradients, limiting the formulation of conservation strategies. Second, although ecological niche models such as MaxEnt and GARP have been widely used in species distribution research, biological modeling research for lampreys is still relatively scarce. Existing studies are mostly limited to local areas or single species, lacking cross-basin and cross-species comparative analysis. Third, most studies are based on short-term surveys (1-2 years), lacking a continuous monitoring network covering the entire life cycle (3-7 years). This makes it difficult to accurately assess population dynamics, age structure changes and adaptive responses under environmental pressure. For example, the correlation mechanism between the habitat preferences of the larval stage (3-4 years) and the distribution of adults is still unclear.

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due to their complex life cycle and cryptic larval stage, their monitoring and research are challenging.

6. Conclusion

Petromyzontiformes are the most primitive extant jawless vertebrates and have important evolutionary biological value. Their global distribution presents an obvious antitropical pattern, mainly concentrated in the temperate waters of the Northern Hemisphere and the mid-to-high latitude waters of the Southern Hemisphere. The distribution and survival of lampreys are strictly restricted by ecological factors such as water temperature, salinity, flow velocity, substrate type and dissolved oxygen, among which low tolerance to water temperature is the key limiting factor for their inability to spread to tropical waters. In recent years, human activities such as habitat fragmentation, dam construction, water pollution and climate change have posed a serious threat to the survival of their populations, with some species facing the risk of local extinction, while a few species have caused ecological damage in invasive areas. Current research combines field sampling, environmental DNA technology and species distribution models to reveal the correlation between their distribution pattern and environmental factors, providing a scientific basis for formulating effective conservation strategies and habitat management measures. Future research should focus on carrying out multi-factor experimental design, quantifying the interactive effects of key environmental factors through the combination of controlled indoor experiments and field observations. It is suggested to construct a multi-scale and multi-species distribution prediction framework, integrate climate models, water system models and ecological niche models to predict the changes in the distribution pattern of lampreys under future climate change, and build a monitoring network covering the main distribution areas to systematically collect data on lamprey population dynamics, environmental factors and human activities. At the same time, promote the integration of multidisciplinary data and knowledge discovery, and apply the research results directly to the practice of lamprey conservation and management. Through the systematic advancement of the above research directions, .these approaches are expected to overcome current research bottlenecks of lamprey distribution research and provide a solid scientific support for the protection of this ancient species

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