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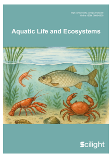

Review

Strontium in Otolith Microchemistry: Mechanisms, Ecological Applications, and Implications for Fisheries Management

Weijie Cui [1,2,3,†], Zhongtang He [1,2,3,†], Mingju Luo [1,2,3], Fengling Zhang [1,2,3], Qun Lu [1,2,3], Jianhu Liu [1,2,3] and Tao He [1,2,3,*]

[1] College of Fisheries, Southwest University, Chongqing 400715, China
[2] Key Laboratory of Freshwater Fish Reproduction and Development (Ministry of Education), Chongqing 400715, China
[3] Key Laboratory of Aquatic Science of Chongqing, Chongqing 400715, China
* Correspondence: hh1985@swu.edu.cn; Tel.: + 86-15023177126
† These authors contributed equally to this work.

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Simple Summary: Fish have small ear stones, known as otoliths, that grow continuously and incorporate chemical elements from the surrounding water. These stones act as natural “black boxes”, recording where a fish has lived and traveled throughout its life. Strontium is one of the most powerful chemical tracers in these stones for tracking migration and identifying fish populations. However, to use this tool effectively, scientists must understand how strontium enters the stone and how environmental factors, such as temperature and salinity, influence this process. This review article summarizes the current scientific understanding of strontium analysis. We explain the biological and environmental mechanisms of strontium deposition and discuss how to interpret these chemical signals accurately. Furthermore, we propose a new framework for applying this knowledge to fisheries management, from tracking broad movements to monitoring individual fish health. This work is valuable because precise tracking of fish stocks is essential for sustainable fishing, protecting aquatic biodiversity, and adapting conservation strategies to a changing global climate.

Abstract: Otoliths, calcified structures in the inner ear of teleost fish, grow incrementally and incorporate chemical elements from the surrounding environment, serving as natural data loggers. Among these elements, strontium (Sr) and its isotopes have become powerful tracers in otolith microchemistry for reconstructing fish life histories, migration patterns, and habitat use. This review synthesizes current knowledge on the principles, applications, and challenges of Sr analysis, bridging biomineralization mechanisms and their practical utility in fisheries science. We first summarize the fundamental mechanisms of Sr incorporation into the otolith matrix, examining key environmental (e.g., water chemistry, salinity, temperature) and physiological (e.g., species-specific metabolism) factors that govern its deposition. We then explore the differential applications of Sr/Ca and $^{87}\text{Sr}/^{86}\text{Sr}$ ratios across diverse aquatic systems, highlighting their effectiveness in resolving complex stock structures and connectivity among freshwater, estuarine, and marine fishes. The review also addresses inherent limitations, including physiological biases and time lags in elemental uptake, which are critical for the accurate interpretation of environmental histories. Finally, we outline future research directions, emphasizing the integration of otolith Sr analysis with advanced ecological modeling to support stock assessment and conservation planning. We conclude that refining Sr-based tools is essential for developing adaptive fisheries management strategies in the face of shifting baselines driven by climate change and anthropogenic pressures.

Keywords: otolith microchemistry; life history; migration; environmental reconstruction; fisheries management; biominerali-zation

1. Introduction

Effective fisheries management and sustainable marine conservation rely heavily on an accurate understanding of stock structure, connectivity, and life history diversity. In an era where climate change is driving unprecedented shifts in species distributions and migration patterns, traditional monitoring techniques—such as physical tagging—often face limitations in spatiotemporal resolution and recapture rates. Otoliths, serving as natural “black boxes”, offer a unique chemical archive to address these complex ecological challenges. As metabolically inert calcium carbonate structures within the inner ear of teleost fish, otoliths grow incrementally and permanently retain chemical elements from the surrounding environment [1,2]. This property transforms them into invaluable tools for reconstructing environmental histories that are otherwise inaccessible.

Each fish possesses three pairs of otoliths: *sagittae*, *lapilli*, and *asterisci*, situated respectively in the *sacculus*, *utriculus*, and *lagena*. These structures interact with sensory hair cells to detect environmental stimuli (Figure 1) [2–4]. Otoliths primarily consist of calcium carbonate in the form of aragonite, calcite, or vaterite, with *sagittae* and *lapilli* mostly composed of aragonite and *asterisci* often consisting of vaterite [5,6]. A defining feature of otoliths is their incremental growth, which forms distinct daily and annual rings through the alternating deposition of protein-rich (opaque) and mineral-rich (translucent) layers [7–9]. Macroscopically, these increments form bands identified by differences in transparency under transmitted or reflected light, which stem from varying ratios of calcium carbonate to organic matter. The inorganic mineral-rich bands are translucent (appearing dark under transmitted light), while the organic matter-rich bands are opaque (appearing bright under transmitted light) [10,11]. The mechanisms associated with the deposition of elements onto otoliths can be predicted by examining the distribution of different elements on the two stripes. At the same time, otoliths are metabolically inert and acellular in growth, and two properties allow for the retention of almost all elements and compounds attached to otoliths. This is precisely why otoliths can be used as a powerful tool for documenting the environments in which fish live [1]. However, this alone does not fully explain the function of otoliths in recording the environment. Numerous studies using elements and compounds from otoliths have been conducted based on the correlation between otolith microchemistry and environmental chemistry, but the exact relationship needs further investigation. The environment where fish are exposed to the water column needs to have a predictable effect on the uptake and attachment of otolithic elements and compounds, and it is only through correlation data such as ratios, contents, or partition coefficients that environmental histories can be reflected [12].

Fish otoliths have become a widely used habitat tracing tool, which is vital for reconstructing fish life history, analyzing fish movements and habitat use, and playing a role in identifying fish populations or groups in different regions [13–17]. While both strontium (Sr) and barium (Ba) are widely used for migration and population identification, their incorporation dynamics differ [6,12]. Barium is often considered a strong indicator of freshwater environments, but its large ionic radius (135 pm) compared to calcium (100 pm) can be a factor, and its reliability as a proxy for factors like water temperature may be limited [18]. In contrast, Sr (ionic radius 118 pm) is structurally more favored for substitution in the aragonite lattice [19]. Although Sr incorporation is complex and influenced by multiple factors, including temperature and physiology, its strong correlation with environmental parameters in many contexts gives it a broad applicability in otolith microchemistry [20–24].

Currently, most studies on Sr in otoliths have focused on marine fishes. In contrast, fewer studies have been conducted on freshwater fishes, and the Sr/Ca ratio and $^{87}Sr/^{86}Sr$ isotope ratio are usually analyzed to reconstruct the fish life history and identify the regional populations. For otolithic trace elements such as Sr, their deposition is usually influenced by environmental factors (temperature, salinity, elemental concentration, etc.) [14,19,25–27]. The use of otolith chemistry for the reconstruction of fish life history and as a habitat tracer is usually based on two assumptions: (1) otolith chemistry reflects the water chemistry of the environment in which fish live; (2) changes in the environment of fish habitats affect the deposition of trace elements in otoliths. The simultaneous establishment of these two hypotheses involves the fundamental ways in which trace elements are deposited in fish otoliths, and current studies have proposed a variety of mechanisms to explain the deposition of trace elements in otoliths: some divalent metal cations (e.g., Sr^{2+}, Ba^{2+}) with large ionic radii can replace Ca^{2+} in the aragonite lattice; trace elements can bind to associated proteins in otoliths and be absorbed by otoliths. As otoliths form increments, daily elements can interact with macromolecular compounds at their edges and be immobilized. Adsorbed ions or cofactors are present as dopants in the lattice interstices [6,19]. In particular, for Sr and Ba, the two most widely used non-essential elements in otolith microchemistry, Sr^{2+}, Ba^{2+} and Ca^{2+} have the same valence state and relatively close ionic radii (100 pm for calcium ions, 118 pm for strontium ions and 135 pm for barium ions) [28,29]. Sr and Ba are often considered direct substitutes for Ca in otolith biomineralization and are mainly influenced by Ca-regulated driving mechanisms in the organism, such as transport in epithelial cells by paracellular pathways via calcium transporter proteins [30–32]. The deposition of any trace element in otoliths is a series of multistage processes, with the basic pathway being the entry of elements from the external environment into the plasma after modulation by some physiological barriers (e.g., gills or intestines). After passing through the plasma into the endolymph, the elements finally contact the endolymphatic fluid with the surface of otoliths to form deposition [1,33]. Although many mechanisms have been proposed to explain trace element deposition, our understanding of the specific physiological processes that regulate elemental deposition in otoliths still lacks a comprehensive understanding, and it is crucial to carry out studies that interconnect physiology with otolith biomineralization processes [32,34].

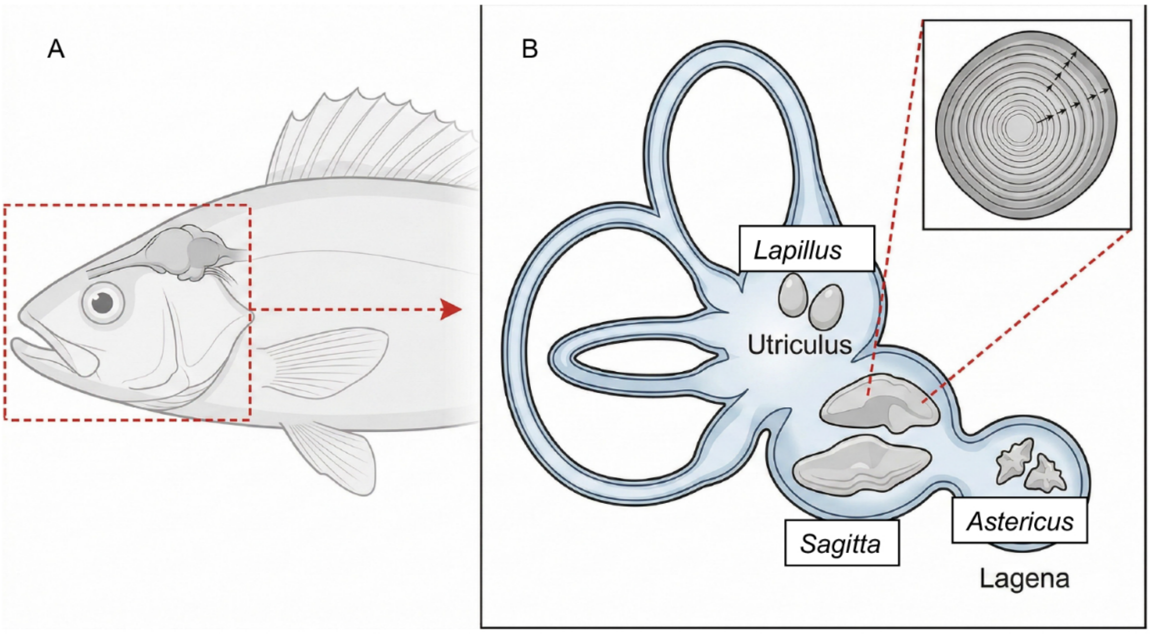


Figure 1. Schematic representation of the teleost inner ear revealing the location of the three otolith pairs: *sagittae*, *lapilli*, and *asterisci*. These metabolically inert calcium carbonate structures act as continuous "environmental data loggers", growing incrementally to permanently record chemical signals (e.g., Sr, Ba) from the surrounding water. The precise extraction and analysis of these structures are the foundational steps for reconstructing individual life histories and assessing stock connectivity.

While the utility of strontium as a tracer is well-established, a disconnect remains between the fundamental understanding of biomineralization mechanisms and the practical interpretation of microchemical data in fisheries science. Current reviews often treat environmental correlations and physiological mechanisms in isolation. This review aims to bridge this gap. We synthesize current knowledge on the environmental and physiological determinants of Sr incorporation, critically evaluating how these factors influence the accuracy of life-history reconstructions in diverse aquatic systems. Beyond summarizing analytical techniques, we highlight the implications of Sr variability for stock identification and propose a hierarchical framework for integrating otolith microchemistry into ecosystem-based fisheries management (EBFM).

2. Applications of Strontium in Biogeography

Strontium in fish otoliths has been widely used in fisheries and ecology, with Sr/Ca, strontium isotope ratios ($^{87}Sr/^{86}Sr$), and strontium partition coefficients (DSr) in otoliths [12,35–41]. Although some studies have focused on such biodynamics of strontium in otolith deposition and uptake mechanisms, the most dominant application still uses Sr in biogeography for fish life history exploration, environmental reconstruction, and habitat tracing [42–45].

2.1. Contrasting Applications in Freshwater, Estuarine, and Marine Environments

In biogeography, the element Sr has now mainly been associated with fish and the environment they inhabit, and in general, Sr/Ca ratios in fish otoliths show a positive correlation with Sr/Ca ratios in the aqueous environment [46–53]. There is a significant difference between freshwater and seawater when using Sr/Ca in otoliths to study fish migration. Since the Sr/Ca ratio in freshwater is generally lower than that in seawater, fish movements can be reflected by the increase or decrease in the Sr/Ca ratio, with a ratio increase representing freshwater-to-sea migration and a decrease in the opposite [54–56]. Although the Sr/Ca ratio in freshwater, an aqueous environment, is usually not as high as that in seawater, in the aqueous environments of a few rivers and lakes with freshwater sources, Sr/Ca can exhibit higher ratios. The Sr/Ca ratios in the otoliths of fishes surviving in these bodies of water can be higher than those in the otoliths of seawater fishes to a certain extent [52]. However, estuarine regions—semi-enclosed coastal bodies where freshwater mixes with seawater—present a significant challenge. The dynamic and variable salinity in estuaries means that otolith Sr/Ca ratios may lack the resolution to clearly distinguish between marine and estuarine habitats, or even between freshwater and estuarine zones [46,57–59]. Interestingly, Ba/Ca, which is often used in conjunction with Sr/Ca for correlation studies, shows the opposite phenomenon, i.e., Ba/Ca ratios are generally higher in freshwater than in marine waters [48], and it may be possible to use Ba/Ca as an alternative to applying Sr/Ca to differentiate poorly between environmental tracers (e.g., where estuarine areas are concerned). By examining inter-individual differences in Sr/Ca ratios in fish otoliths, it would be possible to analyze the water environment experienced by each individual during its lifetime and to visualize the range of salinities experienced by the fish, including seawater, freshwater, or brackish water. In particular, differences in Sr/Ca ratios between the core and peripheral regions of otoliths, or microchemical mapping of Sr and Ca in otolith cross-sections, can be utilized to reflect the movement of fish at various stages of the life cycle (e.g., early developmental stages).

The complexity of estuarine signatures poses a specific challenge for delimiting nursery grounds. Accurate discrimination between estuarine-dependent and marine-transient individuals is crucial for determining the contribution of specific estuaries to the adult offshore stock, which directly informs the prioritization of coastal habitats for conservation.

Despite these successes, the application of Sr/Ca and $^{87}Sr/^{86}Sr$ ratios in biogeography faces inherent limitations. In freshwater systems with homogeneous geology, water chemistry gradients may be insufficient to discriminate between distinct habitats. Additionally, the 'time lag' in elemental deposition—often ranging from 10 to 40 days—can obscure rapid movements between water masses. Relying solely on Sr/Ca ratios without complementary markers (e.g., $\delta^{18}O$ or genetic data) may therefore lead to ambiguous interpretations of stock structure, especially in highly dynamic estuarine environments.

2.2. Tracking Fish Migration

The time for isotopic equilibrium in otoliths varies significantly across species, ranging from a few days to several weeks, depending on factors such as metabolic rate, growth stage, and environmental conditions [60]. Therefore, we can analyze the aquatic environments in which the young of these fishes reside in most cases, especially in the case of amphidromous fishes, such as those from rivers and seas. In the case of amphidromous fish, the $^{87}Sr/^{86}Sr$ ratio change in otoliths should be noticeable when an adult fish growing in a marine or riverine area migrates to another area with a different geological and aquatic environment to spawn. A critical consideration, however, is the 'time lag' required for otolith chemistry to equilibrate with a new environment, which can range from 10 to 40 days. This lag can compromise the accuracy of environmental tracing, particularly if fish move rapidly between water bodies with different Sr concentrations or inhabit highly variable environments like estuaries [51,61]. Application may be somewhat compromised, especially in estuarine waters where a certain amount of temporal variability characterizes daily water chemistry, and the results of analyses using strontium elements may be somewhat biased [12].

2.2.1. Estuarine Waters and the Type of Amphidromous Migration

Heim-Ballew et al. studied native Hawaiian amphidromous fishes [62] by analyzing the changes in Sr/Ca ratios and Ba/Ca ratios in the otoliths to associate with fishes that underwent oceanic migrations in their life histories and found that almost all of these native fishes exhibited amphidromous life histories. However, by analyzing the changes in Sr/Ca ratios before otolith metamorphosis, it was hypothesized that one of them, *Lentipes concolor*, may have some migratory flexibility and that a certain number of this species may have lived their entire lives in freshwater. This result is opposite to the conclusion of previous life history probes for this species [63], suggesting that there is a discrepancy between the life history of Sr/Ca probes and the traditional approach, and may also represent that there is some error in reflecting the migratory type in the change of Sr/Ca ratio. Hwang et al. conducted a study on *Synechogobius hasta* in the upper estuaries of the Kim and Mangyeong rivers in Korea [64] and analyzed the Sr/Ca ratios of its *sagittae* (the mean value of the core region and the outside region of the otolith core). *Synechogobius hasta* (commonly known as the *Javelin goby*) is a euryhaline fish inhabiting brackish estuarine waters in East Asia, often used in migration and habitat tracing studies due to its adaptability to variable salinity environments. The results indicate that the fish has a life history of spawning in estuaries, i.e., brackish water, and inhabiting mainly in estuaries, and emphasize that it does not spawn in freshwater and does not show the main characteristics of amphidromous fish. This study also showed that the fish can experience a wide range of salinities throughout its life and has migratory flexibility, which enables it to survive in a wide range of water environments. Taken together, we can still use Sr/Ca in otoliths to investigate the life history of migratory fish and establish a conservation strategy for the species, linking the Sr/Ca ratio in otoliths to the specific conditions of the aquatic environment. Therefore, appropriate management measures can be taken to minimize the risk of migratory fish in both marine and freshwater environments and to make the effective and sustainable use of the species possible. The observation of partial migration or facultative amphidromy in species like *Lentipes concolor* highlights the need for flexible management frameworks. Static management boundaries may fail to protect the full diversity of life-history contingents, which acts as a 'portfolio effect' buffering stocks against environmental variability.

2.2.2. Migration in the Marine Environment

Among studies that use otolith microchemistry to investigate fish migration, the use of strontium to analyze the migration of marine fish is early and widely used. For example, Zhen Zhao et al. analyzed several data, including Sr/Ca ratio, to investigate the movement pattern of *Dissostichus mawsoni* in the Amundsen Sea, which indicated an individual developmental movement from west to east [65]. In addition, Lae'lien Bassi et al. studied *Reinhardtius hippoglossoides* in the western North Atlantic, analyzed the chemical composition of its otoliths (including strontium), and deduced the migratory patterns and population structure of this species, suggesting a high degree of population connectivity in the region [66]. Of course, given that some current studies suggest that strontium deposition on the otoliths of marine fishes may be more influenced by individual factors than by the environment [12], the use of strontium may be better use in population identification.

2.2.3. Freshwater Environments such as Rivers and Lakes

Dunnigan et al. did some work using the ^{87}Sr/^{86}Sr ratio to analyze the life history, movement pattern, or birthplace of fishes [67]. They analyzed the ^{87}Sr/^{86}Sr ratio in the preserved otoliths of *Lota lota* collected from Koocanusa Lake and its tributaries in the USA in order to trace the natal origin, habitat use, and life history structure of the *Lota lota*. In the analysis, the authors chose the RF (Random forest) model based on previous studies [68–71], and measured the correlation between ^{87}Sr/^{86}Sr ratios in otoliths and ^{87}Sr/^{86}Sr ratios in the corresponding water environment. The two strontium isotope ratios are highly correlated, based on which there is an approximately equal correspondence with *Lota lota* for building RF models. After assigning the *Lota lota* to the corresponding birth area, the relative abundance of the *Lota lota* population has changed over the past four decades. The authors then hypothesized that the establishment of the corresponding dams in this water body may have affected the aquatic ecosystems, resulting in the overall decline in the population of the *Lota lota* and the shift of the types of life histories. Hauser et al. used microchemical analyses of otoliths ^{87}Sr/^{86}Sr to investigate the migration and migratory patterns of the Goliath catfish, *Brachyplatystoma platynemum* in the Amazon River at the individual level, complementing studies of fish movements in the Amazon Basin before and after impoundment, and demonstrated that the migratory patterns of the *Brachyplatystoma platynemum* are different from those of another previously explored fish, the *Brachyplatystoma rouseauxii*, which does not migrate as extensively as the latter and does not involve a return to its birthplace, but still migrates thousands of kilometers in the Amazon basin [72–74]. Due to the widespread construction of dams, hydroelectric plants, and other facilities that intercept fish habitats, it has become a matter of increasing interest to analyze the migratory pathways of some of the migratory species or their return to their spawning grounds and to design conservation strategies based on their population dynamics. As even well-studied species may be missing from the solution of this problem, the use of otoliths and Sr in the water column to analyze fish movements can complement traditional movement studies and may become an important method for analyzing the movement patterns of fish in the future.

Since geological factors highly influence strontium isotope ratios in the water and are not affected by mass fractionation, which can reflect the water column conditions to a great extent and fish otoliths are capable of retaining ^{87}Sr/^{86}Sr ratios in the surrounding aquatic environments they come into contact with throughout their lifetime [75–78], the research method of analyzing the changes in ^{87}Sr/^{86}Sr in otoliths and aquatic systems has been increasingly used in biogeography to track fish species habitats and movement patterns such as migration and migrations [79–81]. Strontium isotope ratios are affected by exogenous and endogenous factors due to the precipitation of Sr in otoliths. While $^{87}Sr/^{86}Sr$ ratios are robust geological tracers, Sr/Ca ratios are influenced by both environmental factors and complex biochemical mechanisms [6]. The study of fish movement patterns using only Sr/Ca ratios (although they are often used in conjunction with Ba/Ca) may be subject to some errors, and strontium isotope ratios can be combined with them for better analysis. Avigliano et al. predictively classified the rivers of the La Plata Basin (South America) by combining the Sr/Ca ratios of the water bodies, the Ba/Ca ratios, and $^{87}Sr/^{86}Sr$ ratios [82], who used Principal Component Analysis (PCA) and Linear Discriminant Analysis (LDA), concluded that the combination of the three was able to more accurately predict the water regime of origin of fishes and the predictive classification was more reliable than using the $^{87}Sr/^{86}Sr$ ratios alone, and that Sr/Ca ratios had a higher impact on the predictive classification than the remaining two, one of the reasons may be that the geological influences in the basin region resulted in some areas where the $^{87}Sr/^{86}Sr$ ratios do not vary much. In this study, a significant positive correlation was also found between the Sr/Ca ratios at the otolith margins and the aqueous Sr/Ca ratios, which contrasts with the non-significant correlation between the Ba/Ca ratios of the two and may indicate that elemental Sr has a better depositional effect on otoliths. This conclusion may be contrary to the relevant chemistry, but from the point of view of the fact that the ionic radius of Sr^{2+} (118 pm) is closer to the ionic radius of Ca^{2+} (100 pm) than Ba^{2+} (135 pm) [28], it seems that the reason for this can be explained by a series of biochemical mechanisms focusing on the uptake and deposition of otoliths of trace metal elements. From the migration of Prochilodus lineatus shown in this study and other conclusions in the literature, it appears that migration pathways can be effectively reflected by correlating the Sr/Ca ratio at the otolith edge with that in the water [83,84].

2.3. Interpreting Strontium Distribution Maps

The otolith edge corresponds to the most recent life cycle [82], whereas the core region of the otolith corresponds to the spawning and early developmental stages of the fish [85,86]. Since the means of determining Sr/Ca is usually a laser-ablation of the core-to-edge otolith cross-section [72], which is perpendicular to the growth-producing sulcus (growth marker) [67], and since trace elements do not break down after deposition in otoliths [14], the counterpart to the previous article is then the otolith core (inside of 50 μm in diameter) and its neighboring area can reflect the environment of the spawning and nursery grounds of the fish [64]. In contrast, the Sr/Ca ratio in the area beyond the otolith core to the otolith edge shows the water environment inhabited by the fish most of the time during the growth phase, and, finally, in the smaller (100 μm) area of the otolith edge, the Sr/Ca ratios may reflect the environment in which the fish inhabited for some time before fishing or before the fish died [72], which may be close to the fishing site, but of course may be separated by a certain distance depending on the movement of the fish.

Many studies have shown that the use of strontium on otoliths (analytical techniques such as EPMA) can be used to explore the life history of fish and to understand the environment of fish at various stages of their lives, and that the use of this method is reliable [87–93]. Using strontium distribution can be an effective alternative to traditional methods for identifying fish migrations, and the environmental history of fish at different life stages can be visualized. Particularly for amphidromous fish, due to the differences in strontium content distribution in different environments at different times, their otoliths usually have multiple distinct areas of strontium content differences, which can be used to analyze their life history patterns. In fact, for general anadromous fish, their otoliths show a “low-high” strontium content change from the core to the edge, corresponding to “freshwater-seawater”, while the opposite is true for general catadromous fish. This method can also be used to identify whether a fish is a single habitat utilization type or to identify wild stocks from farmed and released stocks [93,94]. In addition, even if the fish have a complex migratory history in multiple environments, determining strontium distribution can provide a more reasonable environmental history, which is challenging with other methods. Figures 2–4 characterize the distribution of strontium content in anadromous fish, catadromous fish, and other types (e.g., freshwater-type) of fish, respectively, and the comparison reveals clear differences. Of course, due to the time lag of strontium deposition on otoliths, if fish move rapidly between different water environments, then this type of water environment may not be reflected correctly in the strontium distribution [12,51,61]. In anadromous and catadromous fish, the otolith edges of most individuals do not show the characteristics of the strontium content changes that return to the spawning ground, in which case this method will have a larger error.

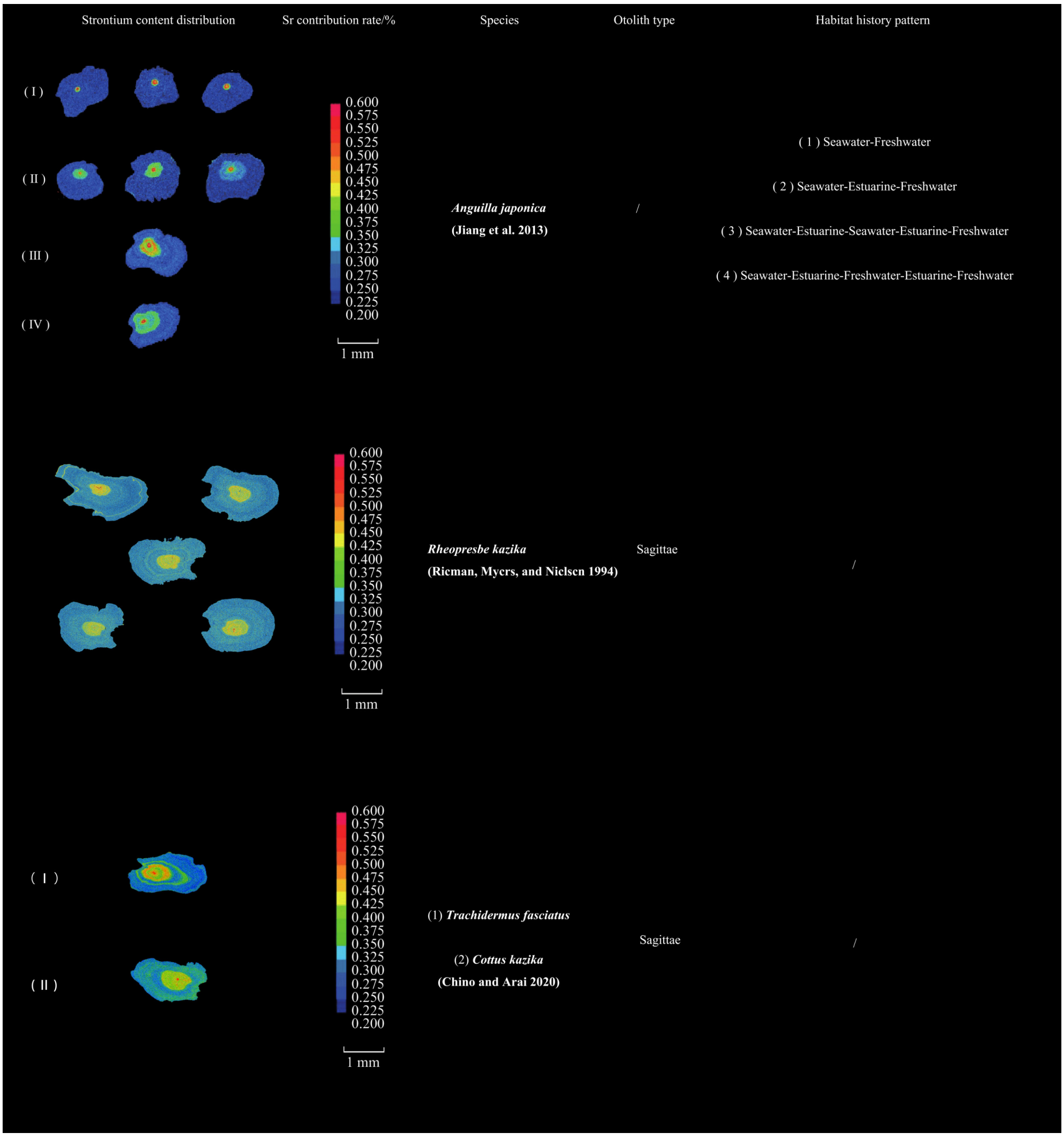
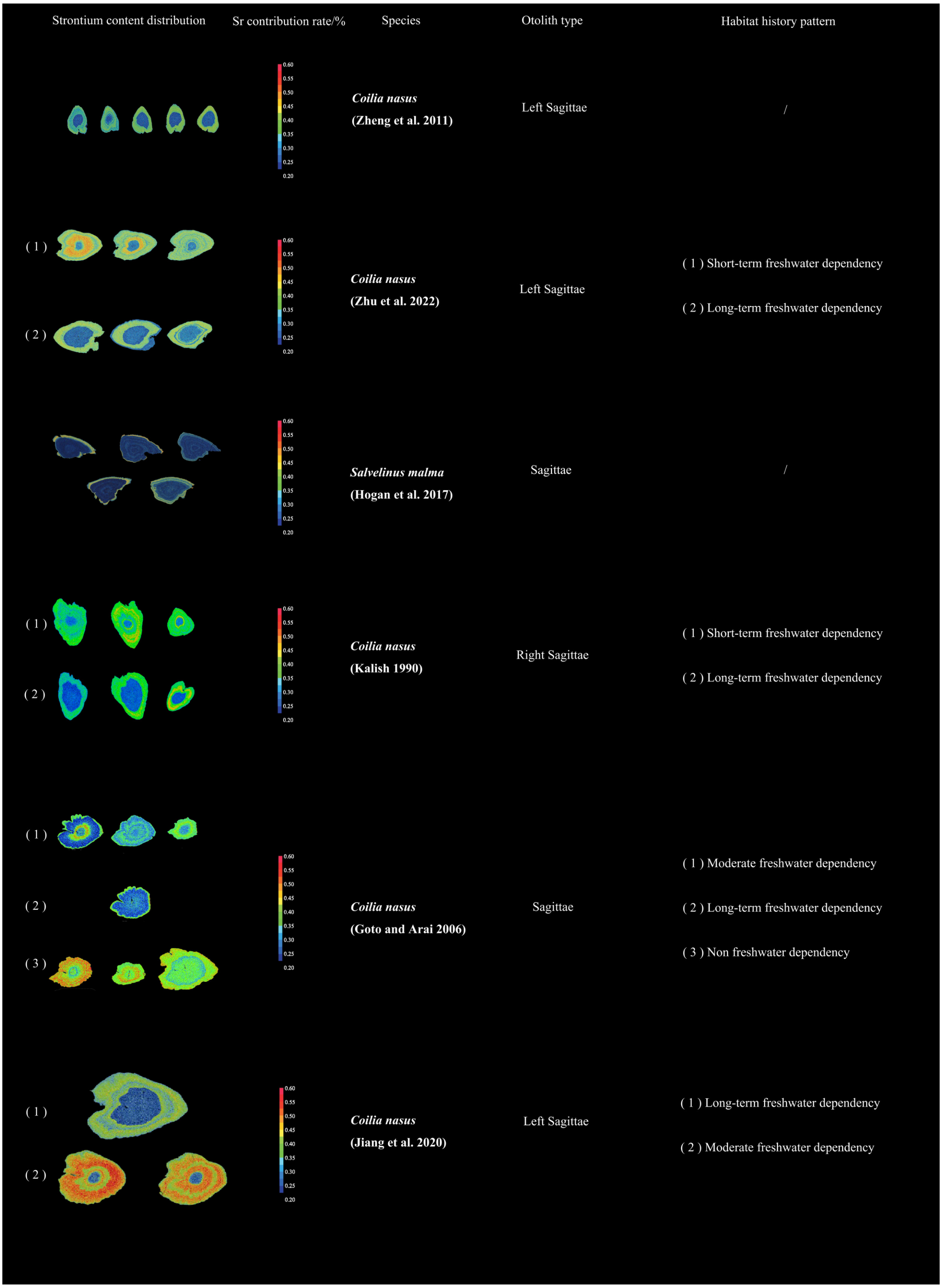


Figure 2. Anadromous strategy (e.g., Salmonids): Characterized by low Sr:Ca ratios in the core (freshwater spawning) increasing to high ratios at the edge (marine migration).

Representative otolith strontium (Sr:Ca) transect profiles distinguishing key fish life-history strategies across salinity gradients. The distinct chemical signatures shown here are critical for discriminating between resident and migratory contingents (partial migration) within a stock, thereby enabling more precise definition of management units.



Strontium content distribution	Sr contribution rate/%	Species	Otolith type	Habitat history pattern
		Coilia nasus **(Zheng et al. 2011)**	Left Sagittae	/
(1) (2)		***Coilia nasus*** **(Zhu et al. 2022)**	Left Sagittae	(1) Short-term freshwater dependency (2) Long-term freshwater dependency
		Salvelinus malma **(Hogan et al. 2017)**	Sagittae	/
(1) (2)		***Coilia nasus*** **(Kalish 1990)**	Right Sagittae	(1) Short-term freshwater dependency (2) Long-term freshwater dependency
(1) (2) (3)		***Coilia nasus*** **(Goto and Arai 2006)**	Sagittae	(1) Moderate freshwater dependency (2) Long-term freshwater dependency (3) Non freshwater dependency
(1) (2)		***Coilia nasus*** **(Jiang et al. 2020)**	Left Sagittae	(1) Long-term freshwater dependency (2) Moderate freshwater dependency

Figure 3. Catadromous strategy (e.g., Anguillid eels): Exhibits high Sr:Ca ratios in the core (marine spawning) decreasing to low ratios during the somatic growth phase in freshwater.

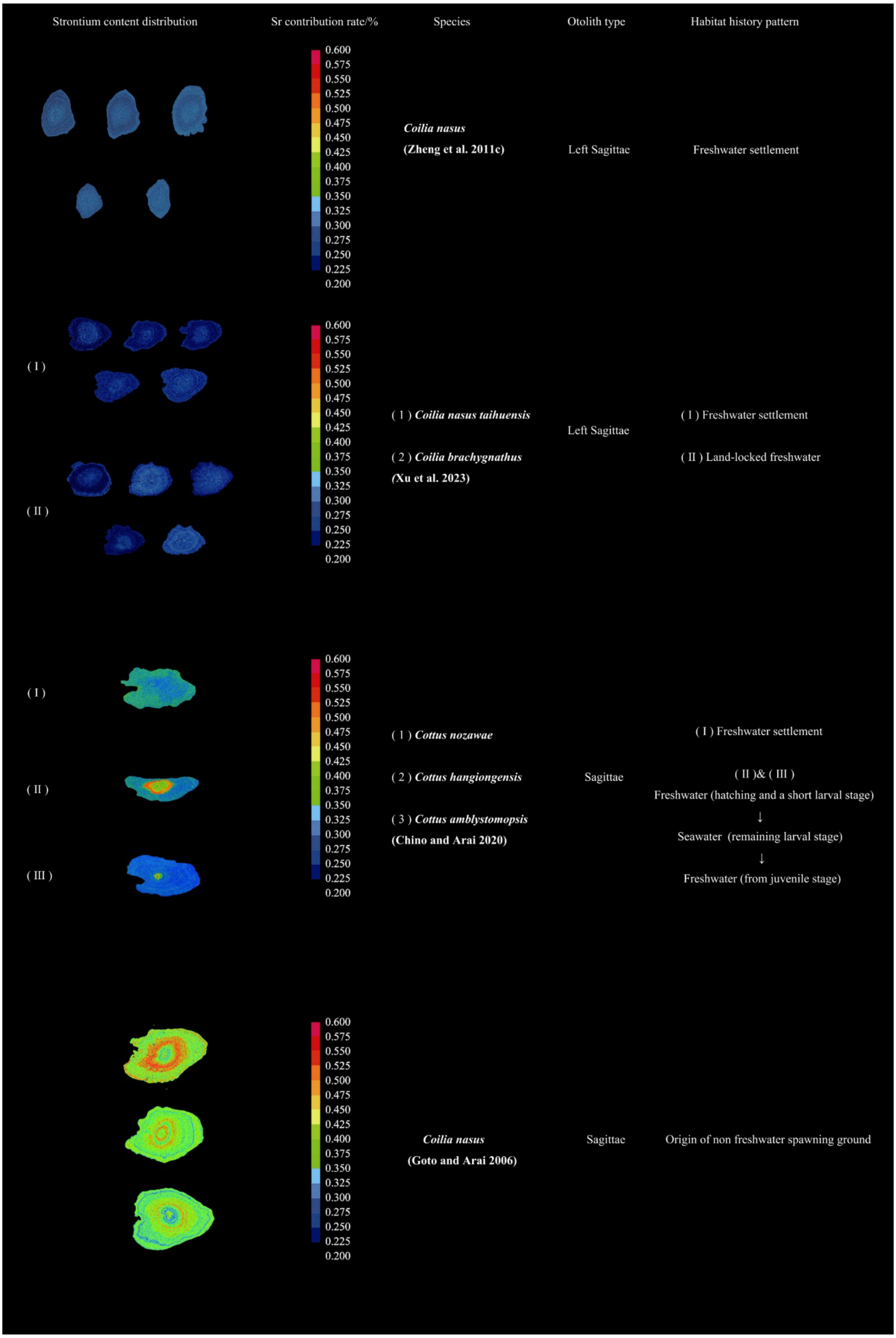


Figure 4. Freshwater resident/Landlocked strategy: Displays consistently low Sr:Ca ratios with minimal oscillation, indicating confinement to freshwater environments throughout the life cycle.

2.4. Other Applications

The partition coefficients commonly used in geochemistry have also been used to quantify the link between trace elements in the environment and in otoliths, the partition coefficient DSr = [Sr/Caotolith]/[Sr/Cawater] for the strontium [12]. Since there are still some problems in analyzing strontium in otoliths and water bodies, this paper will not elaborate on its application in reconstructing the environment.

In terms of population identification, most of the studies using otoliths for identification have been limited to shape indices and Fourier methods, and the combination of otolith microchemistry is still less frequently used; the use of the element Sr has been predominant in these studies, combining microchemistry and morphology to identify fish populations or groups.

Strontium in otoliths can be used not only in biology and ecology, but its concentrations and strontium isotope ratios in the water column can be closely linked to geological factors, especially strontium isotope ratios (^{87}Sr/^{86}Sr). The preservation in natural materials reflects the source of strontium available at the time of their formation, allowing ^{87}Sr/^{86}Sr to be used as a chemical tracer, and this tracing method has already been widely used in the fields of geologic source studies, chronostratigraphy of marine sediments, and other fields [95]. Of course, a tremendous amount of information about geochemical features in modern and ancient environments can be analyzed by linking the Sr/Ca ratio, ^{87}Sr/^{86}Sr ratio, and other data in modern otoliths and fossil otoliths.

3. Environmental Determinants of Strontium Incorporation

The accurate interpretation of otolith Sr signatures requires a thorough understanding of the factors that control their uptake and deposition. These can be broadly categorized as environmental (exogenous) and physiological (endogenous).

3.1. Water Chemistry

Approximately 83% of the strontium in fish otoliths comes from the surrounding aquatic environment [50]. Many studies have shown that the strontium concentration in otoliths (in terms of Sr/Ca ratios) is significantly and positively correlated with the strontium concentration in the aquatic environment. That strontium in the aquatic environment affects the strontium in the otoliths to a significantly greater extent than any other environmental factor [12,46–53]. Many studies have explored the relationship (Table 1) [47,96–103], and barium in the water column may affect the results, so the results would be more accurate if barium in the water column could be eliminated in advance [104]. Regardless of how species are studied, the process of strontium in otoliths needs to be clearly linked to strontium in the water column as a basic prerequisite for conducting experiments.

A meta-analysis of the relevant literature by Izzo et al. [12] showed that strontium concentration in otoliths and strontium concentration in the water column show a significant positive correlation while also being somewhat influenced by other factors, especially ecological niches and that marine fishes usually show a weaker relationship between strontium concentration in otoliths and the aquatic environment than the other ecological niches, which may be related to the fact that strontium elemental deposition in the otoliths of marine fishes (e.g., the Sr/Ca ratio) is dominated by endogenous physiological processes. In contrast, the relationship between strontium concentration in otoliths and the water environment of estuarine fishes showed a large variability, which may be due to the differences in the water conditions of each estuary and the species-specific variability. Meanwhile, the range of strontium concentrations to which fish were exposed shows a significant positive correlation with the magnitude of the association between strontium in otoliths and the water environment.

Table 1. Summary of published linear relationships between water Sr/Ca and otolith Sr/Ca for various fish species under field and laboratory conditions. R² values indicate the strength of the correlation.

Habitat	Species	Salinity	Ba Content	Expression	R^2	Reference
field	Oncorhyncus clarki	/	/	[Sr/Ca]otolith = 0.55[Sr/Ca]water − 0.18	0.96	[46]
	Sperata aor			[Sr/Ca]otolith = 0.211[Sr/Ca]water + 0.749 (mg/g)	0.93	[96]
	Alosa sapidissima			[Sr/Ca]otolith = 0.29[Sr/Ca]water − 0.08	0.99	[97]
				[^{87}Sr/^{86}Sr]otolith = 0.94[^{87}Sr/^{86}Sr]water + 0.04	0.97	
Field and low water flow volumes	Salmo salar			[Sr/Ca]otolith = 0.225[Sr/Ca]water + 0.150	0.97	[98]
				[^{87}Sr/^{86}Sr]otolith = 1.00008[^{87}Sr/^{86}Sr]water	0.99	
Field and high water flow volumes				[Sr/Ca]otolith = 0.303[Sr/Ca]water + 0.162	0.83	
				[^{87}Sr/^{86}Sr]otolith = 1.000002[^{87}Sr/^{86}Sr]water	0.93	
Laboratory	Dicentrarchus labrax	10/20/30	/	[Sr/Ca]otolith = 0.294[Sr/Ca]water − 0.729	0.98	[99]
	Mallotus villosus	30.12 ± 0.033		[Sr]otolith = 154.47[Sr]water + 3931.4	0.98	[100]
	Acanthopagrus butcheri	5	low Ba	[Sr/Ca]otolith = 0.4986[Sr/Ca]water + 1.1131	0.88	[101]
			Medium Ba	[Sr/Ca]otolith = 0.4749[Sr/Ca]water + 0.4807	0.95	
			High Ba	[Sr/Ca]otolith = 0.4504[Sr/Ca]water + 0.3071	0.98	
		32	low Ba	[Sr/Ca]otolith = 0.2028[Sr/Ca]water + 0.9740	0.81	
			Medium Ba	[Sr/Ca]otolith = 0.2457[Sr/Ca]water + 0.6489	0.88	
			High Ba	[Sr/Ca]otolith = 0.2600[Sr/Ca]water + 0.3731	0.94	

Table 1. *Cont.*

Habitat	Species	Salinity	Ba Content	Expression	R^2	Reference
Laboratory	Forsterygion nigripenne	20	low Ba	[Sr/Ca]otolith = 0.1937[Sr/Ca]water + 0.6384	0.99	[102]
			Medium Ba	[Sr/Ca]otolith = 0.1986[Sr/Ca]water + 0.7721	0.99	
			High Ba	[Sr/Ca]otolith = 0.1887[Sr/Ca]water + 0.6485	0.99	
		33	low Ba	[Sr/Ca]otolith = 0.2024[Sr/Ca]water + 1.3784	0.99	
			Medium Ba	[Sr/Ca]otolith = 0.2134[Sr/Ca]water + 1.0548	0.99	
			High Ba	[Sr/Ca]otolith = 0.2537[Sr/Ca]water + 0.6352	0.99	
	Paralichthys olivaceus	31.0 ± 0.12	1Ba (4/4)	[Sr/Ca]otolith = 0.178[Sr/Ca]water + 0.356	0.98	[103]
			2Ba (3/4)	[Sr/Ca]otolith = 0.172[Sr/Ca]water + 0.436	0.99	
			4Ba (2/4)	[Sr/Ca]otolith = 0.211[Sr/Ca]water − 0.185	0.96	
			6Ba (1/4)	[Sr/Ca]otolith = 0.198[Sr/Ca]water + 0.010	0.93	

3.2. Salinity and Temperature

In salinity analyses, the linkage between the water body environment and the isotopes of Sr/Ca and strontium in otoliths $^{87}\mathrm{Sr}/^{86}\mathrm{Sr}$ is based on the premise that there is a correlation between the deposition of trace elements (e.g., Sr, Ba) in the otoliths of fishes and the salinity of the corresponding fish-inhabiting water environment (freshwater, seawater, or brackish water) [56,105–111]. In general, the Sr/Ca ratio in otoliths will be positively correlated with the salinity (and just the opposite for Ba/Ca) in the water environment of the habitat during the corresponding formation period of the region in otoliths [56], which is also able to explain the difference in Sr/Ca ratios between freshwater fishes and seawater fishes in the previous section, as salinity in seawater is much higher than that in freshwater. While stable $^{87}\mathrm{Sr}/^{86}\mathrm{Sr}$ ratios primarily reflect geological source, Sr/Ca ratios are highly sensitive to other environmental factors, notably salinity and temperature. There is a well-established positive correlation between otolith Sr/Ca and salinity, making it a valuable tool for tracking movements across salinity gradients. Similarly, otolith Sr/Ca is often used as a proxy for water temperature, though the nature of this relationship is complex [12].

3.3. Temperature

Although otolith Sr/Ca ratios are frequently explored as potential proxies for water temperature, the relationship is complex, species-specific, and often inconsistent. While some studies report positive correlations (e.g., in *Leiostomus xanthurus*), others find negative or negligible effects (e.g., in Mallotus villosus) (Table 2). It is now a widely accepted consensus that Sr/Ca ratios are primarily driven by ambient salinity and water chemistry [19], with temperature acting as a secondary or confounding factor. The reliability of Sr/Ca as a direct thermometer is considered far inferior to oxygen stable isotopes (δ^{18}O). Consequently, using Sr/Ca to reconstruct temperature histories requires extreme caution and rigorous species-specific calibration to account for significant interspecific differences.

Table 2. Examples of the influence of temperature and salinity on Sr/Ca ratios or the strontium partition coefficient (DSr) in fish otoliths. Arrows (↑ or ↓) indicate a positive or negative correlation, respectively.

Factor	Species	Effect	Expression	Reference
Temperature	*Leiostomus xanthurus*	↑	DSr = 0.0046 T (°C) + 0.089	[17]
	Mallotus villosus	↓	log DSr = −0.026 T (°C) + 0.907	[112]
	Clupea harengus		T (°C) = −2.955 [Sr/Ca] × 1000 + 19.172	[104]
	Gadus morhua		T (°C) = −5.120ln[(Sr/Ca) otolith × 1000/25.145]	[113]
Salinity	*Anguilla japonica*	↑	[(Sr/Ca) × 1000] otolith = 0.091SAL + 3.790	[114]
	Sarotherodon melanotheron		[(Sr/Ca) × 1000] otolith = 1.4188SAL + 0.4015	[115]
	Pogonias cromis		otolith Sr:Ca = 2.134 + 0.019salinity	[116]
	Hucho perryi		[(Sr/Ca) × 1000] otolith = 0.09SAL + 1.93	[117]
	Anguilla marmorata		[(Sr/Ca) × 1000] otolith = 0.141SAL + 1.42	[118]
	Sarotherodon melanotheron		[(Sr/Ca) × 1000] otolith = 0.088SAL + 9.074	[119]

3.4. General Applications of Multifactor Analysis and Variability of Results

As research on the deposition of trace elements in otolith microchemistry has gradually deepened, the vast majority of studies have shifted from unifactorial to multifactorial analyses of environmental factors, and some relatively significant results have also been achieved. In general, the effects of salinity and temperature on the Sr/Ca ratio in otoliths are more obviously species-specific. However, the study by Tian et al. concluded that the efficiency of elemental admixture into otoliths in the water column exhibits a unique response to changes in temperature or salinity that is dependent on the variability of strontium itself and the environmental influences [27]. Collectively, it is more critical to identify environmental factors that can be analyzed with respect to the effects of elemental admixture in fish otoliths. To clearly demonstrate the effects of temperature and salinity on the strontium element in otoliths, a table is provided with rising arrows indicating positive correlations and falling arrows indicating negative correlations (Table 2) [18,104,112–119]. In laboratory studies of the effect of environmental factors on the elemental admixture of otoliths, other variables need to be tightly controlled to prevent influencing the results of the experiments.

4. Physiological Regulation and Biomineralization Mechanisms

4.1. Distribution and Deposition Mechanisms of Strontium

Understanding Sr deposition requires determining its distribution between the otolith's protein-rich matrix and its inorganic mineral (aragonite) layers. Direct analysis is challenging due to difficulties in extracting otolith proteins intact. To circumvent this, Thomas et al. used endolymph, the otolith's growth medium, as a surrogate material [120]. In this study, unlike elements such as Pb, which is distributed only in the protein fraction of endolymph, and Mg, Li, and K, which are distributed only in the salt fraction, Sr is distributed in both the proteinaceous fraction and salt fraction, suggesting that exogenous and endogenous processes could have influenced the deposition of Sr in otoliths. Even though endogenous processes, including but not limited to otolithic metalloproteins interacting with trace metal elements, can reduce the reliability and predictability of otolithic elements for environmental reconstruction in life history reconstruction and habitat tracing studies, Sr is currently the most widely used trace element in environmental reconstruction. The average concentration of Sr in otoliths (10,644 μg/g) is in first place among the 22 trace elements measured, and the concentration in endolymph (7754 μg/g) is also in a high position (6/22). Its enrichment factor (137.27%) is much higher than that of Ba, which is only lower (22.59%), which, in combination with the mechanism of precipitation of Sr as explored by Doubleday et al. [24], could indicate that Sr has a higher rate of calcium substitution in the aragonite lattice than Ba. This result may be due to the greater uptake of Sr by endolymph and otoliths in the biotic uptake kinetics or to the fact that the concentration of Ba in the water environment is lower than that of Sr.

Organic components (consisting of 50% proteins, 30% proteoglycans, and 20% collagen) [121] act as a base matrix for the deposition of calcium carbonate, the main constituent of otoliths, which are continuously distributed throughout the surface of the biomineral, and can influence the deposition and admixture of trace elements such as strontium processes, but for the application of the element strontium, the greatest influence is probably still in the use of the Sr/Ca ratio organic component on Ca calcification deposition [30]. In studies related to reconstructed environments, strontium may be able to bind to metalloproteins in otoliths and be taken up by the otoliths, just as this process may have some influence on the conclusions deduced, since protein binding, an endogenous factor, was not considered while analyzing changes in the ratio [6].

As a biomineral, otolith is composed not only of aragonite but may also be composed of calcite and vaterite. Since these three calcium carbonate isomers are not the same nature, the processes by which trace elements are deposited in them vary somewhat. As previously mentioned, in the case of calcareous deposition or calcification, for the strontium, the crystal structure of aragonite, the principal constituent of most otoliths, is one which is favorable to the admixture of the element and replacement of calcium. To date, strontium continues to be considered most likely to be deposited in otoliths as a calcium substitute via calcium uptake mechanisms in fish [122], and no corresponding strontium transport proteins have been found to exist in Osteichthyes or even vertebrates as a whole [32]. A physiological process of uptake followed by deposition is essential for the element on otoliths, and we can infer the uptake of strontium from the way calcium is taken up by the fish, which is generally via the gills in Osteichthyes [123]. However, it has also been shown that gastrointestinal calcium uptake occurs for specific fishes [124–127].

The metal mass fractionation exhibited in lower organisms such as foraminifera and corals reflects their low physiological limitations for elemental uptake [128]. Loewen et al. suggested that mass fractionation may play a role in the selective uptake of strontium isotopes into the skeletal structure of fishes, resulting in a deviation from the natural abundance of the strontium isotopes in the 88Sr/86Sr ratio deviating from the natural abundance [32]. However, further confirmation is required to determine whether this finding can be applied to otoliths, which are also biominerals. If the link between strontium in the aqueous environment and strontium deposited in otoliths can be more comprehensively analyzed, it may be possible to deduce the potential deposition mechanism of strontium and the specific physiological process of deposition.

4.2. Endogenous Physiological Factors

To quantify the effect of physiological factors on trace elements in otoliths, Sturrock et al. consecutively collected plasma and otoliths from Pleuronectes platessa from corresponding sites and compared the trace element differences between them [34], and found that the effect of physiological factors on otolith composition was very evident in the Sr/Ca ratio, with the Sr /Ca ratio was linearly and positively correlated with the Sr/Ca ratio in plasma, which in turn was influenced by a variety of endogenous factors. Since there is a high probability that elemental strontium in plasma at this stage of entry into otoliths will be realized through the process of transfer to the intermediate medium endolymph, which is an obvious growth medium for otoliths in the inner ear capsule [129], the possibility of further research to establish the mechanism of strontium transfer from otoliths-endolymph-plasma may be an issue to be explored in the future.

Several studies have been conducted to apply strontium isotope ratios to analyze the effects of endogenous and exogenous factors on the element strontium in otoliths. Janak et al. found that by rearing two populations of Oncorhynchus Nerka from different lakes in the same source of water, there were small but significant differences ($U \geq 19$, $p \leq 0.03$) and changes in the $^{87}Sr/^{86}Sr$ ratio in otoliths from yolk uptake to the equilibrium stage of exogenous food were significantly different between the two populations. The presence of discontinuous segments in otolith morphology may serve as a marker for yolk absorption, and the onset of exogenous nutrition in conjunction with strontium variations may be able to make diagnostic results using such markers more reliable [68,129–131]. Ignoring these physiological vital effects can lead to misinterpretation of stock connectivity. For instance, stress-induced changes in Sr uptake could be mistakenly attributed to movement between water masses, potentially leading to the delineation of incorrect management units.

4.3. Biomineralization Differences in Marine and Freshwater Fishes

The partition coefficient approach from the geochemical field may not yield accurate results for studying the association of strontium in fish otoliths and the water environment due to a growing number of studies showing that species differences or individual differences in physiological states may affect strontium deposition in otoliths [34]. Marine fishes may differ from freshwater fishes in terms of either the direct deposition mechanism of strontium or the physiological state that influences strontium deposition. This physiological influence appears to be particularly pronounced in marine fishes. Some studies suggest that even when ambient water chemistry is constant, otolith elemental concentrations in marine species can vary systematically within a population. This implies that in marine environments, endogenous physiological processes may exert a stronger influence on Sr deposition than in freshwater fishes—potentially even exceeding the influence of the external water chemistry. If this holds, it challenges the basic premise that otolith chemistry directly reflects the environment, potentially limiting the utility of Sr/Ca ratios for migratory tracking in fully marine species [34]. However, if physiological processes exert a greater influence on otolith trace elements than the aqueous environment. In that case, the use of trace element/Ca ratios (especially Sr/Ca in marine fishes) for population or group identification of specific fishes may be more successful, which may indicate that freshwater fishes are more reliable when using strontium for studies such as fish migration. In contrast, marine fish have greater accuracy in population or group identification. The success of the use of strontium in otoliths to reconstruct habitat associations or environmental histories depends on the ability to distinguish environmental effects on otolith chemistry from physiological signals [12].

5. Future Directions

Moving forward, integrating otolith Sr analysis with advanced ecological modeling and multidisciplinary tools (e.g., transcriptomics and hydrodynamic models) will be crucial for robust stock assessments.

A significant drawback of traditional otolith analysis is that it requires lethal sampling. Consequently, research has increasingly explored non-lethal alternatives, such as fin rays and scales. While these structures enhance fish welfare, their utility remains debated. Unlike otoliths, which are metabolically inert, fin rays and scales may be subject to elemental resorption or different biomineralization mechanisms. Further validation is essential to determine if fin ray microchemistry can accurately align spatial and temporal environmental records.

6. Conclusions

Strontium microchemistry in otoliths serves as a powerful and indispensable tool for unravelling fish life histories, migratory behaviors, and stock connectivity. The incorporation of Sr is a multifactorial process, primarily governed by environmental salinity and water chemistry, but intricately modulated by species-specific physiological mechanisms [51,132–139].

To maximize the utility of these chemical archives, we propose integrating otolith Sr analysis into a hierarchical fisheries management framework: utilizing $^{87}Sr/^{86}Sr$ for broad-scale geological provenance, and Sr/Ca for tracking fine-scale habitat use across salinity gradients. As climate change and anthropogenic pressures continue to alter aquatic baselines, refining these Sr-based tools will provide the critical, science-based insights needed to adapt conservation strategies and ensure the sustainable management of global fisheries.

Author Contributions

W.C. and Z.H.: conceptualization; W.C.: methodology, data curation; M.L.: software, visualization; W.C., Z.H. and M.L.: validation; F.Z.: formal analysis; Q.L.: investigation; J.L.: resources; W.C. and Z.H.: writing—original draft preparation; T.H.: supervision, project administration, funding acquisition, writing—review and editing. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest

The authors declare no conflict of interest.

Use of AI and AI-Assisted Technologies

During the preparation of this work, the authors used Grammarly to correct grammatical errors. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

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