REVIEW ARTICLE

eISSN 2234-1757

Fish Aquat Sci. 2025;28(9):583-595
https://doi.org/10.47853/FAS.2025.e49

Fisheries and Aquatic Sciences

The application of otolith chemistry in fish life history assessment: review

Tariku Hailu Belay[1, 2, *], Alemken Berihun Mengist[3]

[1] *Department of Fisheries and Aquatic Sciences, College of Agriculture and Environmental Sciences, Bahir Dar University, Bahir P. O. Box 79, Ethiopia*
[2] *Department of Biology, College of Natural and Computational Sciences, Debark University, P. O. Box 79, Ethiopia*
[3] *Department of Wildlife and Ecotourism Management, College of Agriculture and Natural Resources, Gambella University, P. O. Box 126, Gambella, Ethiopia*

Abstract

Understanding the movement and life-history characteristics of marine organisms is vital for effective management and conservation efforts, yet there are still significant knowledge gaps in this field. Understanding how specific nursery habitats shape juvenile behavior and growth, as well as how connectivity influences population dynamics and stock structure, is essential for developing such strategies. Chemical analysis of fish otoliths provides valuable insights into these processes. Otoliths incorporate and store elements from the surrounding environment throughout the fish's life, with their composition reflecting ambient environmental conditions. Elements such as Ba/Ca, Mg/Ca, U/Ca, B/Ca, and Sr/Ca in otoliths show strong correlations with ocean water temperatures and are used to determine population structure, identify estuarine nurseries, and assess connectivity between juvenile and adult populations. Elements like strontium and barium are particularly useful for reconstructing environmental and migration histories for individual fish, as their concentrations reflect local seawater availability. The elemental ratios of otoliths exhibit differences as fish move through different aquatic environments, with higher Sr/Ca ratios found in marine waters and higher Ba/Ca ratios in freshwater. Additionally, there's a positive relationship between otolith Sr content and ambient salinity, although the extent of this relationship depends on water Sr concentrations. Other elements like K, Na, Zn, and Mn are likely influenced by physiological regulation in organisms. Stable isotope analysis of both soft tissues and otoliths provides further insights into the biotic environment, reflecting fish diet and aiding in determining movement within estuaries, migratory patterns, and habitat use.

Keywords: Otolith, Life history, Otolith chemistry

Introduction

Otoliths are paired crystalline structures that are found in the inner ear of all bony fishes which are used for sound reception, equilibrium maintenance, and processing directional cues (Popper & Fay, 2011). Their chemical composition due to a variety of key properties has been increasingly utilized in the field of fish spatial dynamics. Significantly, otoliths show unparalleled

Received: Nov 8, 2024 **Revised:** Dec 23, 2024 **Accepted:** Feb 24, 2025

***Corresponding author:** Tariku Hailu Belay
Department of Fisheries and Aquatic Sciences, College of Agriculture and Environmental Sciences, Bahir Dar University, Bahir Dar P. O. Box 79, Ethiopia
Tel: +251-931165301, **E-mail:** tahailu21@gmail.com

time-keeping properties. Otoliths undertake early development in the fish's life, typically during the embryonic stages and continue to grow gradually through daily deposits of calcium carbonate ($CaCO_3$) aragonitic crystals onto a fibroprotein organic matrix (Athanasiadou, 2018; Payan et al., 2004). Although the exact relationships are not always evident, it is conclusive that otolith composition is predisposed by environmental conditions.

This remarkable phenomenon has been leveraged by studies that employ otolith shape and whole otolith chemistry to deduce stock structure, as well as chemical patterns across growth bands to gather information across various life history stages (Elsdon et al., 2008). In addition, otoliths are present in all teleost species building them especially valuable for studying habitat exploitation in fishes that inhabit inaccessible environments such as deep or remote areas where external tags may not be viable or are unlikely to be recovered (Fairclough et al., 2011).

The capacity of otoliths to document and hold detailed environmental histories throughout an individual fish's lifetime offers a unique chance for geolocating fishes in both time and space. Consequently, otolith microchemistry serves as an enormously valuable resource, allowing for the inference of past conditions, stock structure, connectivity patterns, and individual migration routes. Understanding the spatial structure of fish stocks and their relationships within and between them is progressively recognized as a vital prerequisite for sustainable fisheries management (Athanasiadou, 2018; Botsford et al., 2009). The concept of open marine fish populations with evenly spread individuals in a homogeneous environment is largely outdated. Instead, marine habitats and their inhabitants are documented to have scattered distributions due to spatial and temporal variations in physical and biological structures (Hixon et al., 2002). Identifying such patches poses a particular challenge in the open ocean due to its vast, three-dimensional structure and the scarcity of stable geographical and temporal boundaries. Nevertheless, advancements in satellite telemetry and remote sensing have significantly enhanced the ability to link water masses and their inhabitants (Sims et al., 2006), thus improving our understanding of the migratory behavior of individual fishes (Block et al., 2011). Historically, catch data and mark-recapture experiments have been fundamental in establishing a broad understanding of marine fish distributions. However, the resolution of such data tends to be relatively coarse, with arrangements closely tight to the distribution of fishing fleets (Righton et al., 2010).

The utilization of pop-up satellite archival tags and electronic data storage tags has experienced a significant upwelling over the past decade, driven by advancements in miniaturization and recording capacity. These improvements enable the sometimes multi-year recording of the environmental experiences of individual fishes (Block et al., 2011). These emerging technologies have offered fascinating new perspectives into migratory behaviors and the mechanisms principal population structuring. However, their widespread use is often hindered by cost, battery life, low retrieval rates, and size limitations, resulting in observations primarily limited to the adult phase of uppermost predators. To gain a comprehensive understanding of ontogenetic fish movements, a toolbox approach is essential. This involves employing a variety of independent techniques that offer insights at specific spatial and temporal scales, thus facilitating a deeper understanding of connectivity across different life-history stages (Kaplan et al., 2010). Various natural tags are utilized for this purpose, encompassing stable isotopes in soft tissues, amino acid signatures (Riveiro et al., 2011), molecular genetics (Cook et al., 2007), parasite loadings, phenotypic markers (Lawton et al., 2010; Sequeira et al., 2010), color, and otolith shape, alongside the chemical composition of calcified structures like otoliths and scales (Campana, 1999). Each method has demonstrated potential for determining population structure and distinguishing between resident and migrant fishes. However, otolith chemistry has exhibited the most promise for reconstructing lifetime movements. This technique operates on the fundamental assumption that as the otolith grows, chemical markers from the surrounding environment are assimilated into its microstructure, creating a unique fingerprint that reflects, to some extent, the physicochemical characteristics of the environment in which it originated.

The exact mechanisms governing elemental incorporation into the otolith are still not comprehensively understood (Campana, 1999), and inconsistent patterns of element incorporation among species and studies challenge its routine application to movement reconstruction (Elsdon et al., 2008). The objective of this paper is to offer scientists valuable insights into the migration patterns of fish. When combined with otolith annuli, scientists can also determine the age of fish when they migrated through different water bodies. This information is crucial for comprehending fish life cycles, allowing fisheries scientists to make better-informed decisions regarding fish stocks.

https://doi.org/10.47853/FAS.2025.e49

Otolith Structure

Modern quantitative analyses of the sophisticated details of otolith shape, exterior structures, internal microstructure, and chemical arrangement have related designs that can be distinctly associated with specific and even intra-specific, differences in populations or the environmental histories of individuals (Elsdon et al., 2008). Otoliths mainly consist of aragonite, a polymorph of calcium carbonate. The antecedents of otolith mineralization are all found in the endolymph fluid, where proteins play a crucial role in mediating the size, shape, and orientation of crystal formation (Payan et al., 2004).

Throughout a fish's life, aragonite precipitates continuously but erratically, which leads to the formation of otoliths. A solid structure is formed by the gradual accretion of the otolith caused by biological mediation by proteins connected to the endolymph. This process alternates between concentric bands of mineral-rich (more dense) and mineral-deficient (less dense) zones. Since each band, sometimes referred to as a growth band or growth increment, is usually created over a predictable amount of time (one increment per year, for example), age can be estimated by counting the increments after the formation period is established. Age determination relies heavily on the gradual nature of otolith growth. The environmental and developmental forces that the growing fish encounter are reflected in the biological roots of increment creation. These factors could be anything from regular and seasonal environmental cycles to ontogenetic events that are important for development, like first consuming and reproduction. However, for a biological structure to accurately reflect the passage of time, internal physiological events linked to individual developmental processes and environmental circumstances shouldn't disrupt the regular routine of formation (Begg & Brown, 2000).

Otolith morphology

Insignificant variations in otolith form have been working to determine whether fish have generally resided in different geographic regions from other fish of the same species, indicating potential isolation into distinct "stocks" that may require separate management (Bergenius et al., 2006). Additionally, otolith arrangement can provide understandings into ecological links of collected species by studying otoliths discovered in stomach contents and identifying the species they coined from (Baker & Sheaves, 2005). Otolith morphology can be categorized by numerous approaches, including linear measures (e.g length, breadth), internal otolith measurements (nucleus length, increment width), two-dimensional size measurements (area, perimeter), and outline form analysis. Fourier analysis (FA) has recently been utilized to predict otolith form, generating a series of cosine and sine curves from the coordinates of a traced outline (Bergenius et al., 2006).

It is important to think through several factors that may cause differences in otolith samples, including size, age, sex, and differences in year-class, before attributing variations in otolith shape to environmental influences or indicating distinct stocks. Analyzing otolith shape is beneficial in this aspect because it enables the quick assessment of numerous samples, especially with recent image processing methods. Employing image processing techniques is cost-effective, simplifies image reanalysis, allows for the creation of audit trails, and enhances speed and usability compared to traditional linear morphometric methods (Cadrin & Friedland, 1999).

Conventional methods of examining otolith structures traditionally view otoliths solely as timekeepers, offering only absolute age data and resulting in a singular value for each sampled specimen. This approach requires multiple specimens to provide longitudinal insights into a population. However, detailed observations of internal microstructures have introduced an additional dimension to this basic analytical approach. By conducting validation experiments that delineate the development of specific internal microstructures over time, it becomes feasible to correlate certain time intervals with particular life-history events or pinpoint specific regions within an otolith associated with documented life-history occurrences. For example, awareness of the timing of artificial marking or the documented capture date of a specimen enables researchers to trace back through the otolith to internal features that would have formed during specific events, such as the onset of maturation or periods of documented environmental disruption.

Identifying unique characteristics of otoliths associated with documented events can potentially enable these features to serve as proxies for similar events in otoliths from other individuals. This line of research presents numerous opportunities for delving into various facets of a fish's otherwise concealed life history. For instance, growth patterns during early developmental stages can be inferred by measuring the widths of clearly defined otolith increments deposited in the fish's early years (Elsdon et al., 2008). Otolith morphology can be characterized using various methods, including: 1. Linear measurements: such as length and width. 2. Internal otolith measurements: such as nucleus length and increment width. 3. Two-dimensional size measurements: such as area and perimeter. 4. Outline shape analysis: examining the overall shape of the otolith.

Furthermore, FA has been utilized to model otolith shape. This technique entails generating a sequence of cosine and sine curves derived from the coordinates of a traced outline, offering a precise mathematical portrayal of the otolith's shape (Bergenius et al., 2006). Addressing potential sources of variation among otolith samples, such as differences in size, age, sex, and year-class, is crucial before attributing disparities in otolith morphology to environmental factors or as indicators of distinct stocks. Otolith shape analysis presents a valuable approach, as it permits the swift examination of numerous samples, particularly with modern image processing methods. Shape analysis techniques leveraging image processing are relatively cost-effective, simplify image reanalysis, enable the creation of audit trails, and provide enhancements in speed and user-friendliness compared to traditional linear morphometric techniques (Cadrin & Friedland, 1999). These advantages make otolith shape analysis a powerful tool for studying population dynamics and stock structure in fish populations.

Comparing wavelet and fourier transformation methods for otolith shape analysis

Otolith morphometry is preferred over the traditional method of morphometric and meristic characters of the fish body because otoliths are usually not affected by the short-term changes in fish condition or preservation of samples (Campana & Casselman 1993; Neves et al., 2023). Geometric outline and landmark methods are commonly used to study otolith shape variations between or among fish groups by removing size-dependent variation using an allometric approach (Stransky, 2014). Otolith shape variation analysis by geometric outline method involves capturing otolith outline and deriving Cartesian coordinates (x, y) using image analysis tools like scanning electron microscopy, light microscopy, TPSDig, MorphoJ and ImageJ (Stransky, 2014). Several methods are being used for fitting outlines; however, the FA is most commonly employed (Özpiçak et al., 2024; Stransky, 2014) but has limited applicability for otoliths which show significant and complex curvatures. The issues with FA can be alleviated by using Elliptical Fourier analysis (EFA) which decomposes the complex curves of otoliths by generating the sum of harmonically related ellipses (Crampton, 1995; Stransky, 2014; Tracey et al., 2006;). The Wavelet transform can be used as a substitute to the usually applied Fourier transform. Moreover, the Wavelet transform can resolve the problem of poor estimation of sharp edges of otoliths associated with Fourier transform (Libungan & Pálsson, 2015). The software products for FA of 2D outlines are HANGLE, HMATCH, and HCURVE (Crampton & Haines, 1996) while for EFA, EFAwin (Isaev MA & Denisova, 1995), SHAPE package (Iwata & Ukai, 2002; Sadighzadeh et al., 2012), and ShapeR and Momocs packages in the R environment (Brophy et al., 2016; Denechaud et al., 2020; Libungan & Pálsson, 2015) are commonly used. The Shape R package is more common as it has been specifically designed for otolith shape study while Momocs on the other hand is used for general image and shape analysis.

Otolith composition

The analysis of fish otolith composition is becoming increasingly important for fisheries researchers. The calcium carbonate making up the otolith mainly comes from the surrounding water. As the otolith grows, new calcium carbonate crystals form. Just like any crystal structure, there are spaces in the lattice during crystal formation, allowing trace elements from the water to attach to the otolith. Examining the trace elemental composition or isotopic signatures of these trace elements within a fish otolith offers clues about the water environments where the fish previously lived (Patterson et al., 1993). The utilization of fish otoliths dating back as far as 172 million years has simplified the examination of the habitats where the fish flourished. Furthermore, robotic micromilling devices have been utilized to retrieve extremely detailed records of the fish's life history, including diet, temperature variations throughout its life, and its birthplace. One of the most extensively researched trace and isotopic signatures is strontium, thanks to its similarity in charge and ionic radius to calcium (Patterson et al., 1993).

However, researchers can delve into more specific signatures by analyzing multiple trace elements within an otolith. A commonly employed technique for this purpose is laser ablation inductively coupled plasma mass spectrometry, which can measure various trace elements simultaneously. Alternatively, a secondary ion mass spectrometer can be utilized, offering higher chemical resolution but capable of measuring only one trace element at a time. Finfish (class Osteichthyes) possess three pairs of otoliths: sagittae (singular sagitta), lapilli (singular lapillus), and asterisci (singular asteriscus). The sagittae, being the largest, are positioned just behind the eyes and are approximately level with them vertically. The lapilli and asterisci (the smallest of the three pairs) are located within the semicircular

https://doi.org/10.47853/FAS.2025.e49

canals. Typically, the sagittae and lapilli are made of aragonite, although vaterite abnormalities can occur (Reimer et al., 2016), while the asterisci are typically composed of vaterite. The shapes and relative sizes of the otoliths vary among fish species. Generally, fish from highly structured habitats such as reefs or rocky bottoms (e.g., snappers, groupers, many drums, and croakers) exhibit larger otoliths compared to fish that spend most of their time swimming rapidly in straight lines in the open ocean (e.g., tuna, mackerel, dolphinfish).

Flying fish have notably large otoliths, possibly due to their need for balance while leaping out of the water to "fly" through the air. Often, distinct morphological features of an isolated otolith can help identify the fish species. Throughout their lives, fish otoliths accumulate layers of calcium carbonate and a gelatinous matrix. The rate of accumulation varies with the fish's growth, typically slowing during winter and accelerating during summer, forming rings reminiscent of tree rings. By counting these rings, the fish's age in years can be determined. Typically, the sagitta, being the smallest of the three pairs of otoliths, is used for age and growth studies. Moreover, in many species, the accumulation of calcium carbonate and gelatinous matrix alternates on a daily basis, allowing for the determination of fish age in days (Boss, 1999). This additional data, often acquired under a microscope, yields valuable insights for early life history studies. Measuring the thickness of individual rings has been employed in certain species to estimate fish growth, as it's been assumed that fish growth correlates directly with otolith growth. However, some studies have challenged this assumption, showing that there isn't always a direct relationship between body growth and otolith growth. In instances of reduced or no body growth, otoliths may continue to accumulate, suggesting that the direct correlation might be with metabolism rather than growth itself (Nazir & Khan, 2021).

Otoliths, in contrast to scales, maintain their structure even during periods of reduced energy intake, rendering them an invaluable tool for determining the age of fish. Although fish continue to grow throughout their lives, the growth rate typically slows down in mature individuals. Consequently, the rings formed in otoliths during later life stages tend to be closer together. Moreover, a small proportion of otoliths in certain species may exhibit deformities as they age. Studies on the age and growth of fish are essential for understanding various phenomena including the timing and extent of spawning, recruitment patterns, habitat preferences, duration of larval and juvenile stages, and the overall age distribution within populations. This understanding is crucial for formulating effective fisheries management strategies (Lackmann et al., 2019).

Thus far, researchers have identified 50 different elements within otoliths, yet only seven of these elements—Li, Mg, Mn, Cu, Zn, Sr, and Ba—are commonly utilized to deduce past fish locations. This preference stems from the diverse environmental conditions and the fact that the concentrations of these elements in otoliths often surpass detection thresholds. In seawater, ions of hard acids like Li^+, Mg^{2+}, Ca^{2+}, Sr^{2+}, and Ba^{2+} form robust bonds with hydroxyl groups radicals, primarily existing as hydrated free ions. Typically, these ions exhibit longer residence times compared to the ocean's mixing duration, leading to fluctuations in their concentrations based on salinity variations. Conversely, soft and intermediate acid ions such as Cu^{++}, Zn^{++}, and, to a lesser degree, Mn^{++}, bind to softer bases like Cl^- and CO_3^- in seawater. These bonds are relatively weak, rendering soft elements reactive and easily soluble in sea water (Henderson, 1984; Nazir & Khan, 2021).

The precise relative bioavailability of various elements for uptake in marine fishes remains poorly understood. Nevertheless, it is probable that these elements undergo fractionation during their transport across the gut, gills, and skin. In marine species, osmoregulation primarily takes place across gut membranes, thereby ensuring relatively stable concentrations of blood Ca, Na, K, Mg, and Cl. This occurs consistently across both marine and freshwater fishes, despite notable disparities in ambient concentrations of these elements (Campana, 1999). Following their entry into the circulatory system, the transport, availability, and eventual destiny of elements are contingent upon their chemical properties, metabolic necessities, and the constitution of the blood fluid. Elements that serve as integral components of functional enzymes or structural tissues are inclined to have extended mean residence times within the body, owing to the continual recycling of enzymes and tissues. Conversely, elements lacking significant structural or physiological roles may undergo rapid elimination, resulting in short residence times. Nevertheless, exceptions exist, notably with quintessentially toxic metals like Cd, Pb, and Hg, which exhibit prolonged residence times due to comparatively inefficient excretion mechanisms (Williams, 1971).

Consequently, the sequence of elemental alterations along an otolith might indicate variances in turnover durations and the quantity of body reservoirs for those specific elements. Elements characterized by brief turnover durations, like Mn and Ba, could be more suitable for scrutinizing intricate temporal variations compared to elements potentially entailing longer turnover durations, such as Sr and Pb. Within blood plasma, soft acid cations like Cu^{++} and Zn^{++}, and conceivably Mn^{++}, are actively bound to histidine, methionine, and cysteine residues of plasma proteins. These elements are employed in metabolic processes or are actively conveyed to the liver for subsequent excretion. According to Williams (1971), less than 10% of the total blood Cu is presumed to exist in plasma as the free ion. Conversely, around 50% of the total Ca and Sr are approximated to be present in plasma as the free ion.

Consequently, there is a high likelihood of fractionation between hard and soft acid ions within the blood plasma. Magnesium (Mg) may display somewhat distinct behavior in comparison to other Group II elements due to its small ionic radius, except when hydrated, at which point it enlarges significantly. Additionally, Mg has been associated with stabilizing amorphous mineral phases during otolith biomineralization and, owing to its participation in various biological processes, is rigorously regulated within the body (Weiner, 2008). The ever-changing nature of metal ion speciation in blood plasma suggests that the makeup of blood, including its proteins and their ratios, could impact the ratio of free ions. Consequently, this may affect their capability to traverse the barrier between plasma and endolymph. Variations in the types and amounts of blood plasma proteins are expected to have a greater impact on the ions classified as soft acids, given their stronger connection with these proteins. Nevertheless, there's a notable decrease in major elements in the endolymph, leaving primarily potassium (Kalish, 1991) indicates active discrimination against most ion types by the saccular epithelium (Payan et al., 2004).

According to the hard and soft acid-base theory, soft metals tend to exhibit strong binding affinities with proteins, which suggests that they are likely to be incorporated into the otolith while bound to the organic matrix. This notion is supported by observed spatial variations in otolith copper (Cu), as documented by Milton et al. (2000), where an estimated 70–100% of Cu and 40–60% of otolith zinc (Zn) are linked with the protein matrix. The integration of these metals into the otolith mineral phase can occur through various mechanisms: (1) substitution for Ca, influenced by factors such as ion charge, radius, and crystal elasticity, (2) incorporation within dislocation sites on the crystal surface during growth, potentially influenced by kinetic factors like precipitation rate, or (3) potentially through inclusion in amorphous precursor mineral phases, as suggested by Weiner (2008).

The process of element fractionation during incorporation into the otolith becomes even more complex due to the additional influence of temperature. There is ongoing debate regarding whether these temperature effects are direct or indirect, with numerous studies suggesting that they may be linked to physiological mechanisms such as growth rate, which in turn are influenced by ambient temperature. Walther et al. (2010) discuss potential mechanisms driving "growth rate effects" on otolith microchemistry, dividing them into two main categories: kinetic and physiological. Kinetic theories propose that accelerated growth at higher temperatures results in increased entrapment of trace element impurities into the developing crystal, facilitated by the faster growth and higher prevalence of crystal defects (Gaetani & Cohen, 2006).

Another kinetic hypothesis posits that increased calcification rates lead to a higher influx of Ca^{++} ions into the endolymph, thereby diluting other elements in the precipitating fluid. However, while studies have demonstrated that crystal growth rate impacts elemental partitioning in abiotic $CaCO_3$ formation, biogenic $CaCO_3$ undergoes formation via a transient amorphous phase associated with the organic matrix (Weiner, 2008). Consequently, direct extrapolation of patterns from inorganic crystal theory may be deceptive. Moreover, the physiological hypothesis revolves around the synchronization of somatic growth rates with protein synthesis, wherein significant alterations in the protein composition of biological fluids influence the availability of ions for absorption into the otolith (Kalish, 1991). This suggests that fluctuations in somatic growth rates may indirectly affect the integration of elements into the otolith by modifying the availability of ions for absorption.

Several studies have reported that the otolith chemistry is influenced by environmental factors (e.g., water chemistry, temperature, salinity, and their interactive effects) and physiological processes (e.g., growth, metabolism, and reproductive stage) (Elsdon & Gillanders, 2003; Gaetani & Cohen, 2006; Mazloumi et al., 2017; Stanley et al. 2015; Sturrock et al. 2014; Walsh & Gillanders, 2018; Walther et al., 2010). Therefore, the knowledge of how exogenous and endogenous factors affect otolith chemistry is essential to reconstruct the life history events and the migration pattern of fish species (Elsdon et al., 2008; Reis-Santos et al., 2013). The predominant source of the elements incorporated into the otoliths is the ambient water but for some elements such as Zn the main source is diet thereby the relative contribution may vary for different elements (Doubleday et al., 2013; Walther & Thorrold, 2006). The ambient water chemistry is

https://doi.org/10.47853/FAS.2025.e49

regulated by several factors such as underlying geology, anthropogenic influences, precipitation, agricultural runoff, mixing of different water bodies, etc. (Elsdon et al., 2008). Therefore, the chemical composition may vary between water bodies or even within a water body at temporal and spatial scales (Elsdon et al., 2008; Kerr et al., 2007). Moreover, otoliths permanently record spatial and temporal variability in water chemistry (Campana et al., 2000; Dorval et al., 2005; Mateo et al., 2010; Miller, 2007).

Otolith microchemistry

The integration of microchemical composition analysis has introduced a new dimension to otolith studies. While the fundamental carbonate structure of otoliths consists of aragonite, trace elements can be assimilated into the aragonite lattice during formation, akin to any crystalline material. Examining the elemental or isotopic composition of an otolith often correlates with the levels of such elements in the habitats inhabited by individual fish. This correlation yields valuable insights into the environmental conditions encountered by the fish throughout its life history. Simultaneous measurement of various trace elements enhances the ability to differentiate specific elemental signatures associated with different water bodies (Xu et al., 2023). Chemical analysis of an otolith, through discrete sampling of microchemical trace elements across a section, can unveil seasonal or inter-annual patterns in otolith chemistry, indicating developmental migrations through diverse waters. Moreover, advancements in employing this archival information can enhance the age validation of wild-caught fish. A notable application is the utilization of radioactive isotopes stemming from historical nuclear weapons testing, incorporated onto otoliths as markers of known past events, enabling subsequent increment formation to be calibrated.

Importance of Otolith Chemistry to Fisheries Management

Data extracted from otoliths, when coupled with metrics like fish size, weight, and reproductive status, can be employed to calculate various parameters crucial for effectively regulating fish stocks. At its core, an otolith offers insights into the number of growth rings formed prior to sampling, thereby approximating the fish's age at capture, provided the frequency of ring formation is known. This age data gains significance within a management framework when supplemented with additional biological insights and basic mathematical models describing the composition and behavior of the harvested population. Through the integration of otolith findings with other ecological and environmental data, fisheries managers can enhance their comprehension of population demographics, growth patterns, recruitment dynamics, and stock composition, facilitating more informed and sustainable management strategies (Beverton & Holt, 1957; Nazir & Khan, 2021).

The amalgamation of fish length and age data enables the depiction of a broad trajectory of lifetime growth for typical individuals in the population and facilitates the computation of growth rates. Incorporating sex and reproductive status into growth data aids in establishing an age-fecundity correlation and discerning sex-specific growth patterns. Moreover, by merging age estimates derived from otoliths with counts of fish per age category in a sample, alongside the influx of fish into each age category annually (age-specific recruitment), survivorship and thus mortality rates can be determined. These assessments furnish fisheries analysts and managers with a spectrum of insights delineating the exploitable fish stock (Nazir & Khan, 2021). When applied to previously untapped fish stocks, such insights offer an estimation of potential productivity, serving as a basis for calculating sustainable yield. Additionally, employing the age-specific fecundity relationship, the number of eggs from each cohort can be ascertained, with total egg production computed to forecast recruitment for the following year through a stock-recruitment relationship (Beverton & Holt, 1957). These insights are critical for effective fisheries management and conservation efforts.

The age-fecundity relationship provides valuable insights into the varying contribution of reproductive fish across different age groups to the yield of the subsequent cohort. By correlating age with the number of fish captured, estimated through catch and effort monitoring, catch-at-age data can be derived. Examining these data across different fishing years enables the identification of alterations in the demographic makeup of the exploited fish stock, potentially signaling instances of growth overfishing. This analysis is pivotal for detecting shifts in population structure and guiding adaptive management approaches aimed at safeguarding the sustainability of fishery resources.

Between 1955 and 1970, the global catch from wild harvest fisheries surged significantly from 30 million to 70 million tonnes. In 2022, fisheries and aquaculture production reached an all-time high of 223.2 million tons (FAO, 2024). However, this rapid expansion in fishing activity has had far-reaching consequences on target species and ecosystems, resulting in declines in harvested populations worldwide, a trend evident since at least the late 1980s, and possibly earlier (Pauly, 1987). Fisheries and natural resource managers now grapple with numerous challenges as fish stocks continue to dwindle. Fishing fleets, overcapitalized from various countries, operate across oceans, targeting catches from diminishing stocks. Additionally, illegal, unregulated, and unreported fishing practices further exacerbate the sustainability crisis in fisheries globally. While technological advancements have bolstered fishing efficiency and sustained catch rates in temperate fish stocks for many decades, similar advancements have only recently reached tropical fisheries. Subsistence fishing assumes a crucial role, serving as a vital, and in some cases, the principal source of animal protein for local communities.

It has been proposed that certain tropical fish stocks, particularly those linked with coral reefs, are more susceptible to exploitation compared to temperate fish stocks due to the multi-species, multi-gear, and multi-sectoral nature of the fisheries that exploit them, as well as the specific life history traits of the fish. These challenges underscore the pressing need for sustainable fisheries management approaches to safeguard the long-term well-being of marine ecosystems and the livelihoods of coastal communities. The diverse array of life-history characteristics among tropical fish species, coupled with escalating exploitation, extensive transportation, and international marketing, introduces complexity to the management of tropical fisheries. While scientifically grounded national management practices have been implemented in recent decades, there is a growing emphasis on comprehending the impacts of fishing and associated harvest strategies. Management agencies and local governments are increasingly investing in promoting sustainable fishing practices.

Research endeavors are broadening to parameterize the life history characteristics of target species, delineate stock structure, and comprehend migration patterns aimed at safeguarding harvested stocks and their critical habitats. Foundational demographic data, particularly when employed in age-based stock assessments, have been pivotal in numerous fisheries management decisions in temperate regions and are increasingly sought after for tropical species. Many commonly targeted tropical species exhibit long lifespans, relatively small sizes, and attain maximum size at relatively young ages. These attributes constrain the applicability of traditional length-based stock assessment methods, underscoring the importance of fish aging for prudent management. One of the foremost challenges encountered by fisheries managers is acquiring information that delineates the historical and current status of fisheries and the fish stocks they rely on. The application of this information is paramount in ensuring future harvests are sustainable (Arim & Naya, 2003). This emphasizes the criticality of ongoing research, data gathering, and adaptive management strategies to navigate the intricacies of tropical fisheries and preserve marine resources for posterity.

The Application of Otolith Chemistry in Fish Life History Assessment

To identify marine species

Despite the physiological differences between marine, euryhaline, and freshwater fishes, particularly in osmoregulation, laboratory studies indicate little inherent difference in otolith element incorporation mechanisms (Walther & Thorrold, 2006). This suggests that otolith chemistry can be a reliable tool for identifying marine species. While seawater Sr:Ca ratios exhibit little variation, ontogenetic effects on otolith Sr:Ca ratios are often observed in species spending part of their lifecycle in saltwater, especially during significant metabolic events like metamorphosis (Walther et al., 2010). Despite this, otolith Sr:Ca ratios in marine fishes show considerable interspecific differences, generally increasing with age (Kalish, 1989; Walther et al., 2010), and intra-annual fluctuations often surpass those seen in diadromous species. While various factors like temperature, age, growth rates, stress, and gonad maturation have been implicated, no single causal factor has been identified for these patterns.

It's intriguing that in adult marine fishes like blue grenadier, Australian salmon, and bearded rock cod, factors such as growth rate and reproductive investment seem to exert a stronger influence on otolith Sr:Ca ratios than ambient temperature. However, the lack of systematic experimental works examining the relationship between temperature and otolith Sr:Ca across a full reproductive cycle leaves some questions unanswered. The correlations observed between otolith Sr:Ca ratios and physiological parameters such as gonadosomatic index and plasma protein concentrations in species like *P. barbatus* suggest that variations in protein composition during gonad development could affect the availability and uptake of Sr into the otolith. Similarly, in red drum and Atlantic salmon, fluctuations in otolith Sr:Ca ratios were linked to spawning activity and gonad maturation, respectively. These physiological influences on

https://doi.org/10.47853/FAS.2025.e49

otolith element ratios could complicate interpretations of movement patterns and stock discrimination. However, they also offer potential for understanding reproductive biology, such as onset of sexual maturity and reproductive investment (Clarke & Friedland, 2004).

For diet research

The resilience of fish otoliths to digestion renders them invaluable tools for dietary research, as they can be found intact in the digestive tracts and feces of seabirds and piscivorous marine mammals. By identifying otoliths recovered from these sources, researchers can reconstruct the prey composition of marine mammal and seabird diets. Additionally, segregating retrieved otoliths into right and left allows for the estimation of the minimum number of prey individuals ingested for a given fish species. Otolith size can also be utilized to retrospectively calculate prey size and biomass, thereby aiding in the estimation of marine mammal prey consumption and potential impacts on fish stocks (Arim & Naya, 2003).

Certainly, relying solely on otoliths for estimating cetacean or pinniped diets presents challenges due to potential erosion in the digestive tract, which can skew measurements of prey number and biomass. Fragile otoliths are particularly susceptible to underestimation in the diet. To address these biases, otolith correction factors have been devised through captive feeding experiments. These experiments involve feeding seals fish of known size, enabling the quantification of otolith erosion for different prey taxa (Grellier & Hammond, 2005). Complementing otolith analysis with other informative skeletal elements like fish vertebrae, jaw bones, teeth, and distinctive bones enhances prey identification and quantification, especially for species with delicate otoliths, such as Atlantic mackerel and Atlantic herring (Browne et al., 2002).

For characterizing a single population

Gathering age-related information is frequently done to understand the development and mortality patterns among individuals in a harvested population. This aids in devising sustainable harvesting approaches through assessments of stock or evaluations of management strategies. Normally, age data help in understanding how populations change over time within a fishery area or jurisdiction under specific management protocols. When collecting samples for otolith extraction, it's vital to ensure a diverse representation across the fishing area to adequately capture the population's makeup. Although there may be variations in population dynamics within the fishery area, they are often not explicitly taken into account, and instead, average growth and mortality patterns are uniformly applied throughout the region (Kritzer et al., 2001). Certainly! Describing a population entails gathering a specimen sample that mirrors the distribution of individuals across different size, age, or growth categories observed in the natural population. This representative sample guarantees an accurate depiction of all facets of the wild population. Attaining such accuracy involves sampling individuals in alignment with their prevalence in the wild population. Employing random sampling techniques or gear with an equal likelihood of capturing any individual, regardless of its specific traits, ensures the acquisition of a representative sample (Andrew & Mapstone, 1987).

Indeed, attaining a sampling approach completely devoid of selectivity is challenging and often not practical. Nonetheless, compensating for biases resulting from gear selectivity and ensuring representative samples are crucial endeavors. Properly distributing sampling efforts across the region of interest is vital for obtaining unbiased estimates of parameters. While it's impractical to sample every subset of a domain, spreading sampling activities across the domain's spectrum aids in capturing various factors that influence age estimates or derived parameters. Allocating sampling efforts randomly, stratifying them based on environmental conditions, or adhering to systematic patterns like transects or a grid assists in ensuring comprehensive coverage (Andrew & Mapstone, 1987).

Longevity/ontogeny

Conclusively, achieving a sampling approach entirely free from selectivity is indeed difficult and often not feasible. However, recompensing for biases arising from gear selectivity and ensuring representative samples are essential tasks. Effectively distributing sampling efforts across the area of interest is crucial for obtaining unbiased estimates of parameters. While it is impracticable to sample every subset of a domain, spreading sampling activities across the domain's range helps in capturing various factors influencing age estimates or derived parameters. Assigning sampling efforts randomly, stratifying them based on environmental conditions, or following systematic patterns like transects or grids aids in ensuring thorough coverage (Buckland et al., 2015).

Sampling the largest individuals available is often the most effective method for estimating longevity, as larger individuals are more likely to be older. However, in tropical fish species showing “table-top” growth, where individuals reach their maximum size relatively early in life, sampling numerous large individuals may be necessary to accurately estimate maximum age or long life. Estimating the age of transitional life history events, as opposed to terminal ones, presents greater challenges as it necessitates prior understanding of the species’ biology to pinpoint the appropriate target, such as size range, for sampling (Green et al., 2009).

Initially sampling a few individuals across a broad range of characteristics and then concentrating intensive sampling on the approximate sizes at which crucial ontogenetic events occur can be a moderately efficient strategy (Houde et al., 2022). This approach enables researchers to analyze data from the initial samples to determine the sizes at which significant events, like maturity or sex change, take place. While deriving such metrics from a comprehensive representative sample is preferable, the targeted strategy may be more feasible in scenarios with limited resources. For instance, it can suffice for establishing straightforward regulations such as minimum size limits or gear regulations to ensure individuals have adequate time to reproduce before being harvested (Green et al., 2009; Houde et al., 2022).

To determine origin of catches to represent a fishery harvest

Sampling fishery catches can yield valuable insights into the characteristics of the harvested population, but it’s crucial to acknowledge that fishing activities themselves introduce biases into the sample (World Bank, 2012). Fishers often utilize selective gear targeting specific sizes or species, and they may operate in convenient or accessible areas, resulting in a non-random sample of the population. Consequently, even samples collected from catches in an unbiased manner may inherit biases from the fishing process. To mitigate biases associated with sampling fishery catches, several measures can be implemented. For example, it is crucial to avoid selectively sampling specimens based on market value, as this could introduce bias related to specific attributes of low-value fish. Additionally, ensuring that samples are collected from a diverse range of fishers across different ports or areas of the fishing grounds helps to more accurately capture variations in the population (Green et al., 2009).

Randomly sampling specimens from the catch of multiple fishers across different locations or from a diverse range of fishers working on the fishing grounds is an effective approach to avoid biases. This method ensures that the sample accurately reflects the characteristics of the harvested population. Employing a sequence of random numbers to select specimens from the catch provides a straightforward way to implement random sampling and minimize bias. Indeed, tailoring the sampling strategy to leverage any prior sorting of the catch is crucial for ensuring representative sampling (Lohr, 2021). If the catch has been sorted by size or location of capture, the sampling approach should align with this sorting to preserve representativeness. This ensures that the collected sample accurately mirrors the composition of the harvested population across various size classes or fishing areas. By distributing the sampling effort among the sorted size classes or fishing areas, comprehensive coverage of the fishing grounds can be attained, thereby enhancing the reliability of the collected data (Carpentieri, 2019).

Conclusion

The paper discusses the importance of understanding the movement and life-history characteristics of marine organisms for effective management and conservation, particularly in near shore ecosystems such as estuaries and marine habitats serving as nursery grounds. These areas play a vital role in supporting fish and invertebrate diversity and productivity. However, escalating anthropogenic pressures pose threats to these coastal ecosystems, necessitating effective conservation and management strategies. Chemical analysis of fish otoliths is emphasized as a valuable tool for acquiring essential knowledge about fish populations. Otolith microchemistry, particularly elemental composition, reflects environmental conditions, assisting in determining population structure, defining estuarine nurseries, and assessing connectivity between juvenile and adult populations. Elements like Ba/Ca and Sr/Ca ratios in otoliths exhibit correlations with ocean water temperatures and salinity, enabling reconstructions of environmental histories and migration patterns. Stable isotope analysis of otoliths and soft tissues further provides insights into fish diet, movement within estuaries, and migratory behavior. Overall, the paper underscores the importance of otolith chemistry in elucidating the dynamics of marine populations and emphasizes the urgent need for effective conservation measures to safeguard coastal ecosystems facing mounting anthropogenic pressures.

Competing interests

No potential conflict of interest relevant to this article was reported.

Funding sources

https://doi.org/10.47853/FAS.2025.e49

Not applicable.

Acknowledgements
Not applicable.

Availability of data and materials
Upon reasonable request, the datasets used in this study can be made available from the corresponding author.

Ethics approval and consent to participate
Not applicable.

ORCID
Tariku Hailu Belay https://orcid.org/0000-0002-4720-6124
Alemken Berihun Mengist https://orcid.org/0009-0007-9694-1241

References

Andrew NL, Mapstone BD. Sampling and the description of spatial pattern in marine ecology. Oceanogr Mar Biol Ann Rev. 1987;25:39-90.

Arim M, Naya DE. Pinniped diets inferred from scats: analysis of biases in prey occurrence. Can J Zool. 2003;81:67-73.

Athanasiadou D. Nanostructure of calcareous biominerals and osteopontin [Doctoral dissertation]. Montreal: McGill University; 2018.

Baker R, Sheaves M. Redefining the piscivore assemblage of shallow estuarine nursery habitats. Mar Ecol Prog Ser. 2005;291:197-213.

Begg GA, Brown RW. Stock identification of haddock *Melanogrammus aeglefinus* on Georges Bank based on otolith shape analysis. Trans Am Fish Soc. 2000;129:935-45.

Bergenius MAJ, Begg GA, Mapstone BD. The use of otolith morphology to indicate the stock structure of common coral trout (*Plectropomus leopardus*) on the Great Barrier Reef, Australia. Fish Bull. 2006;104:498-511.

Beverton RJH, Holt SJ. On the dynamics of exploited fish populations. London: H.M. Stationery Office; 1957.

Block BA, Jonsen ID, Jorgensen SJ, Winship AJ, Shaffer SA, Bograd SJ, et al. Tracking apex marine predator movements in a dynamic ocean. Nature. 2011;475:86-90.

Boss A. Tidal transport of flounder larvae (*Pleuronectus flesus*) in the River Elbe, Germany. Arch Fish Mar Res. 1999;47:47-60.

Botsford LW, Brumbaugh DR, Grimes C, Kellner JB, Largier J, O'Farrell MR, et al. Connectivity, sustainability, and yield: bridging the gap between conventional fisheries management and marine protected areas. Rev Fish Biol Fish. 2009;19:69-95.

Brophy D, Haynes P, Arrizabalaga H, Fraile I, Fromentin JM, Garibaldi F, et al. Otolith shape variation provides a marker of stock origin for north Atlantic bluefin tuna (*Thunnus thynnus*). Mar Freshw Res. 2016;67:1023-36.

Browne P, Laake JL, DeLong RL. Improving pinniped diet analyses through identification of multiple skeletal structures in fecal samples. Fish Bull. 2002;100:423-33.

Bryant PJ. Biodiversity and conservation: a hypertext book. Irvine, CA: School of Biological Sciences, University of California; 2002.

Buckland ST, Rexstad EA, Marques TA, Oedekoven CS. Distance sampling: methods and applications. Cham: Springer; 2015.

Cadrin SX, Friedland KD. The utility of image processing techniques for morphometric analysis and stock identification. Fish Res. 1999;43:129-39.

Campana SE. Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Mar Ecol Prog Ser. 1999;188:263-97.

Campana SE, Casselman JM. Stock discrimination using otolith shape analysis. Can J Fish Aquat Sci. 1993;50:1062-83.

Campana SE, Chouinard GA, Hanson JM, Fréchet A, Brattey J. Otolith elemental fingerprints as biological tracers of fish stocks. Fish Res. 2000;46:343-57.

Carpentieri P. Monitoring the incidental catch of vulnerable species in Mediterranean and Black Sea fisheries: methodology for data collection. Rome: Food and Agriculture Organization of the United Nations (FAO); 2019.

Choat JH, Axe LM. Growth and longevity in acanthurid fishes; an analysis of otolith increments. Mar Ecol Prog Ser. 1996;134:15-26.

Clarke LM, Friedland KD. Influence of growth and temperature on strontium deposition in the otoliths of Atlantic salmon. J Fish Biol. 2004;65:744-59.

Cook BD, Bunn SE, Hughes JM. Molecular genetic and stable isotope signatures reveal complementary patterns of population connectivity in the regionally vulnerable southern pygmy perch (*Nannoperca australis*). Biol Conserv. 2007;138:60-72.

Crampton JS. Elliptic Fourier shape analysis of fossil bivalves:

some practical considerations. Lethaia. 1995;28:179-86.

Crampton JS, Haines AJ. Users' manual for programs HANGLE, HMATCH, and HCURVE for Fourier shape analysis of two-dimensional outlines. Sci Rep. 1996;96:1-28.

Denechaud C, Smoliński S, Geffen AJ, Godiksen JA. Long-term temporal stability of northeast Arctic cod (*Gadus morhua*) otolith morphology. ICES J Mar Sci. 2020;77:1043-54.

Dorval E, Jones CM, Hannigan R, van Montfrans J. Can otolith chemistry be used for identifying essential seagrass habitats for juvenile spotted seatrout, *Cynoscion nebulosus*, in Chesapeake Bay? Mar Freshw Res. 2005;56:645-53.

Doubleday ZA, Izzo C, Woodcock SH, Gillanders BM. Relative contribution of water and diet to otolith chemistry in freshwater fish. Aquat Biol. 2013;18:271-80.

Elsdon TS, Wells BK, Campana SE, Gillanders BM, Jones CM, Limburg KE, et al. Otolith chemistry to describe movements and life-history parameters of fishes: hypotheses, assumptions, limitations and inferences. Oceanogr Mar Biol Annu Rev. 2008;46:297-330.

Fairclough DV, Edmonds JS, Lenanton RC, Jackson G, Keay IS, Crisafulli BM, et al. Rapid and cost-effective assessment of connectivity among assemblages of *Choerodon rubescens* (Labridae), using laser ablation ICP-MS of sagittal otoliths. J Exp Mar Biol Ecol. 2011;403:46-53.

Food and Agriculture Organization of the United Nations (FAO). The state of world fisheries and aquaculture 2024. Rome: FAO; 2024.

Gaetani GA, Cohen AL. Element partitioning during precipitation of aragonite from seawater: a framework for understanding paleoproxies. Geochim Cosmochim Acta. 2006;70:4617-34.

Green BS, Mapstone BD, Carlos G, Begg GA. Tropical fish otoliths: Where to Next? In: Green BS, Mapstone BD, Carlos G, Begg GA, editors. Tropical Fish Otoliths: Information for Assessment, Management and Ecology. Dordrecht: Springer; 2009.

Grellier K, Hammond PS. Feeding method affects otolith digestion in captive gray seals: implications for diet composition estimation. Mar Mamm Sci. 2005;21:296-306.

Henderson P. Inorganic geochemistry. Oxford: Pergamon; 1984.

Hixon MA, Pacala SW, Sandin SA. Population regulation: historical context and contemporary challenges of open vs. closed systems. Ecology. 2002;83:1490-508.

Houde ED, Able KW, Strydom NA, Wolanski E, Arula T. Reproduction, ontogeny and recruitment. In: Whitfield AK, Able KW, Blaber SJM, Elliott M, editors. Fish and fisheries in estuaries: a global perspective. Hoboken, NJ: John Wiley & Sons; 2022.

Isaev MA, Denisova LN. The computer programs for shape analysis of plant leaves. In: Proceedings of the Mathematics Computer Education International Conference; 1995; Pushchino, Russia.

Iwata H, Ukai Y. Shape: a computer program package for quantitative evaluation of biological shapes based on elliptic Fourier descriptors. J Hered. 2002;93:384-5.

Kalish JM. Determinants of otolith chemistry: seasonal variation in the composition of blood plasma, endolymph and otoliths of bearded rock cod *Pseudophycis barbatus*. Mar Ecol Prog Ser. 1991;74:137-59.

Kaplan IC, Levin PS, Burden M, Fulton EA. Fishing catch shares in the face of global change: a framework for integrating cumulative impacts and single species management. Can J Fish Aquat Sci. 2010;67:1968-82.

Kerr LA, Secor DH, Kraus RT. Stable isotope (δ^{13}C and δ^{18}O) and Sr/Ca composition of otoliths as proxies for environmental salinity experienced by an estuarine fish. Mar Ecol Prog Ser. 2007;349:245-53.

Lackmann AR, Andrews AH, Butler MG, Bielak-Lackmann ES, Clark ME. Bigmouth buffalo *Ictiobus cyprinellus* sets freshwater teleost record as improved age analysis reveals centenarian longevity. Commun Biol. 2019;2:197.

Lawton RJ, Wing SR, Lewis AM. Evidence for discrete subpopulations of sea perch (*Helicolenus ercoides*) across four fjords in Fiordland, New Zealand. NZ J Mar Freshw Res. 2010;44:309-22.

Libungan LA, Pálsson S. ShapeR: an R package to study otolith shape variation among fish populations. PLOS ONE. 2015;10:e0121102.

Lohr SL. Sampling: design and analysis. 3rd ed. London: Chapman and Hall/CRC; 2021.

Mateo I, Durbin EG, Bengtson DA, Kingsley R, Swart PK, Durant D. Spatial and temporal variation in otolith chemistry for tautog (*Tautoga onitis*) in Narragansett Bay and Rhode Island coastal ponds. Fish Bull. 2010;108:155-61.

Mazloumi N, Doubleday ZA, Gillanders BM. The effects of temperature and salinity on otolith chemistry of King George whiting. Fish Res. 2017;196:66-74.

Miller JA. Scales of variation in otolith elemental chemistry of juvenile staghorn sculpin (*Leptocottus armatus*) in three Pacific Northwest estuaries. Mar Biol. 2007;151:483-94.

https://doi.org/10.47853/FAS.2025.e49

Milton DA, Tenakanai CD, Chenery SR. Can the movements of barramundi in the Fly River Region, Papua New Guinea be traced in their otoliths? Est Coast Shelf Sci. 2000;50:855-68.

Nazir A, Khan MA. Using otoliths for fish stock discrimination: status and challenges. Acta Ichthyol Piscat. 2021;51:199-218.

Neves J, Veríssimo A, Santos AM, Garrido S. Comparing otolith shape descriptors for population structure inferences in a small pelagic fish, the European sardine *Sardina pilchardus* (Walbaum, 1792). J Fish Biol. 2023;102:1219-36.

Özpiçak M, Saygın S, Yılmaz S. Comparative otolith morphology in two species of Salmo genus from Türkiye. Ege J Fish Aquat Sci. 2024;41:8-15.

Patterson WP, Smith GR, Lohmann KC. Continental paleothermometry and seasonality using the isotopic composition of aragonitic otoliths of freshwater fishes. Geophys Monogr Ser. 1993;78:191-202.

Pauly, D. Morgan, G.R. Length-based methods in fisheries research . ICLARM Conf Proc. 1987;13:468.

Payan P, de Pontual H, Boeuf G, Mayer-Gostan N. Endolymph chemistry and otolith growth in fish. Comptes Rendus Palévol. 2004;3:535-47.

Popper AN, Fay RR. Rethinking sound detection by fishes. Hear Res. 2011;273:25-36.

Reimer T, Dempster T, Warren-Myers F, Jensen AJ, Swearer SE. High prevalence of vaterite in sagittal otoliths causes hearing impairment in farmed fish. Sci Rep. 2016;6:25249.

Reis-Santos P, Tanner SE, Elsdon TS, Cabral HN, Gillanders BM. Effects of temperature, salinity and water composition on otolith elemental incorporation of *Dicentrarchus labrax*. J Exp Mar Biol Ecol. 2013;446:245-52.

Righton DA, Andersen KH, Neat F, Thorsteinsson V, Steingrund P, Svedäng H, et al. Thermal niche of Atlantic cod *Gadus morhua*: limits, tolerance and optima. Mar Ecol Prog Ser. 2010;420:1-13.

Riveiro I, Guisande C, Iglesias P, Basilone G, Cuttitta A, Giráldez A, et al. Identification of subpopulations in pelagic marine fish species using amino acid composition. Hydrobiologia. 2011;670:189-99.

Sadighzadeh Z, Tuset VM, Valinassab T, Dadpour MR, Lombarte A. Comparison of different otolith shape descriptors and morphometrics for the identification of closely related species of Lutjanus spp. from the Persian Gulf. Mar Biol Res. 2012;8:802-14.

Sequeira V, Gordo LS, Neves A, Paiva RB, Cabral HN, Marques JF. Macroparasites as biological tags for stock identification of the bluemouth, *Helicolenus dactylopterus* (Delaroche, 1809) in Portuguese waters. Fish Res. 2010;106:321-8.

Sims DW, Witt MJ, Richardson AJ, Southall EJ, Metcalfe JD. Encounter success of free-ranging marine predator movements across a dynamic prey landscape. Proc R Soc B Biol Sci. 2006;273:1195-201.

Stanley RRE, Bradbury IR, DiBacco C, Snelgrove PVR, Thorrold SR, Killen SS. Environmentally mediated trends in otolith composition of juvenile Atlantic cod (*Gadus morhua*). ICES J Mar Sci. 2015;72:2350-63.

Stransky C. Morphometric outlines. In: Cadrin SX, Kerr LA, Mariani S, editors. Stock identification methods. 2nd ed. New York, NY: Academic Press; 2014. p. 129-40.

Sturrock AM, Trueman CN, Milton JA, Waring CP, Cooper MJ, Hunter E. Physiological influences can outweigh environmental signals in otolith microchemistry research. Mar Ecol Prog Ser. 2014;500:245-64.

Tracey SR, Lyle JM, Duhamel G. Application of elliptical Fourier analysis of otolith form as a tool for stock identification. Fish Res. 2006;77:138-47.

Walsh CT, Gillanders BM. Extrinsic factors affecting otolith chemistry: implications for interpreting migration patterns in a diadromous fish. Environ Biol Fish. 2018;101:905-16.

Walther BD, Kingsford MJ, O'Callaghan MD, McCulloch MT. Interactive effects of ontogeny, food ration and temperature on elemental incorporation in otoliths of a coral reef fish. Environ Biol Fish. 2010;89:441-51.

Walther BD, Thorrold SR. Water, not food, contributes the majority of strontium and barium deposited in the otoliths of a marine fish. Mar Ecol Prog Ser. 2006;311:125-30.

Weiner S. Biomineralization: a structural perspective. J Struct Biol. 2008;163:229-34.

Williams DR. The metals of life. London: Van Nostrand Reinhold; 1971.

World Bank. Hidden harvest: the global contribution of capture fisheries. Washington, DC: World Bank; 2012. Report No.: 66469-GLB.

Xu Q, Ren Q, Jiang T, Jiang C, Fang L, Zhang M, et al. Otolith microchemistry reveals various habitat uses and life histories of Chinese gizzard shad *Clupanodon thrissa* in the Min River and the estuary, Fujian province, China. Fish Res. 2023;264:106723.