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Relationship between Otolith and Fish Sizes: Validation Using Their 3D Shape Analysis

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Abstract

Nearly one million otoliths, the calcified structures of the inner ear in teleost fish, are sampled annually in the world for the stock assessment. The analysis of internal otolith measurements is based on the idea that there is a relationship between fish size and otolith size and that this proxy is representative of the whole shape of the otolith. In this study, the relationship between fish total length (TL) and five morphometric parameters extracted to the 3D shape otolith analysis, are examined: length (OL), width (OW), height (OH), area (OA) and volume (OV), based on a set of 104 otoliths belonging to 22 species from the English Channel and the North Sea. The otoliths were scanned in three dimensions using an X-ray microtomography, and the relationships were modelled using an allometric log-linear model. The results reveal significant relationships for all metrics ($p < 0.001$), with coefficients of determination (R^2) ranging from 0.500 to 0.656. In the multi-species pooled model, otolith width ($R^2 = 0.656$) proved to be the most robust predictor of fish size, slightly outperforming 3D metrics such as area ($R^2 = 0.617$) and volume ($R^2 = 0.580$). Otolith length ($R^2 = 0.556$) was less accurate than three-dimensional metrics. But given the limited sample sizes per species, these allometric trends should be viewed as preliminary, necessitating larger datasets for species-specific validation. The usual morphometric parameters, such as otolith length, are significant proxies of the whole shape of the otolith. These results suggested the common idea that otolith length is a useful indicator, but otolith width must be considered for greater accuracy and 3D metrics for more detailed shape information. However, the combination of species with varying ecologies and growth rates influences data dispersion and highlights the need for species-specific calibrations. These findings confirm the relevance of otolith metrics for estimating fish size and strengthen their utility in trophic ecology, paleoecology, and fisheries management studies.

Keywords

Otolith Shape, Allometry, 3D, Fish Growth

1. Introduction

Otoliths are calcified structures located in the inner ear of teleost fish, playing an essential role in hearing and balance functions [1]. Composed mainly of aragonite, they grow by the successive deposition of daily or seasonal layers, thus forming precise biological archives of the fish's life [2]. Due to this gradual increment, otoliths are widely used in fish biology and ecology to determine age, individual growth, and to trace environmental or trophic signatures recorded during the life cycle [3] [4].

A fundamental characteristic of otoliths is that their growth rate is not strictly proportional to that of the fish's body. Indeed, several studies have shown that the relationship between body size and otolith dimensions generally follows an allometric pattern, often described by an exponential or power function [5]-[7]. This relationship allows otoliths to be used as indirect proxies for fish size or weight, which is of major interest in a variety of applied fields.

In trophic ecology, the analysis of stomach contents or regurgitated pellets from piscivorous predators often relies on the identification of isolated or fragmented otoliths [8] [9]. Establishing reliable relationships between otolith dimensions and prey body size is therefore essential for estimating the size structure of consumed populations. Similarly, in archaeology and palaeoecology, the good preservation of otoliths in sediments makes them valuable indicators for reconstructing past fish communities and inferring ancient environmental conditions [10]. Finally, in fisheries management, such relationships enable the estimation of fish size from otoliths shape, particularly when whole specimens are not available in samples [11].

In this study, the relationship between the total length (TL) of fish and five morphometric variables of the otoliths whole shape (*i.e.* 3D shape analysis of otoliths) are studied: length (OL), width (OW), height (OH), area (OA), and volume (OV). It is hypothesized that these parameters exhibit allometric growth relative to body size, but with varying degrees of correlation depending on the metric considered. The main objective is to identify which otolith morphological parameters are the best predictors of fish size and the significant proxies of this whole shape, in order to improve their use in trophic ecology, archaeology, and fisheries resource management. Unlike most previous studies, which are limited to two-dimensional measurements, we include three-dimensional metrics such as area and volume to evaluate their relevance as morphometric indicators of body size.

2. Methodology

2.1. Data

The dataset used in this study comes from morphometric measurements of fish and their otoliths. In total, 104 otoliths belonging to 22 fish species from the English Channel and the North Sea, during the French scientific surveys, *i.e.* the Channel Ground Fish Survey 2021 (CGFS) [12] and 2022 [13], and the International Bottom Trawl Survey 2022 survey (IBTS) [14], were analysed (**Table 1**). The otoliths were scanned in three dimensions using an X-ray microtomography, following the protocol in previous study [15].

Table 1. Sampling details of fish length (Total Length, TL in cm) by each fish species.

Fish species	Total number	Min TL	Max TL	Median TL	Mean TL	SD TL
Chelidonichthys cuculus	5	10.20	44.60	27.60	28.28	14.33
Chelidonichthys lucerna	5	10.80	29.70	19.20	20.24	7.96
Clupea harengus	5	15.00	31.80	23.30	23.48	7.16
Dicentrachus labrax	5	35.90	65.70	49.60	50.32	11.22
Engraulis encrasicolus	5	7.00	15.10	11.00	11.00	3.09
Gadus morhua	5	15.60	90.00	51.30	52.58	29.87
Limanda limanda	5	9.00	28.00	20.00	19.20	7.46
Melanogrammus aeglefinus	5	14.20	73.20	44.90	43.54	23.11
Merlangius merlangus	3	10.00	32.70	20.10	20.93	11.37
Microstomus kitt	5	15.40	40.70	27.00	27.22	10.09
Mullus surmuletus	4	13.70	33.30	23.15	23.33	8.19
Platichtys flesus	5	21.00	40.00	33.00	31.80	7.85
Pleuronectes platessa	5	10.00	43.50	29.80	28.08	13.36
Sardina pilchardus	5	14.50	23.00	19.00	19.00	3.41
Scomber scombrus	3	16.30	38.10	22.00	25.47	11.31
Scophtalmus rhombus	5	21.00	59.00	31.00	35.20	15.37
Scopthalmus maximus	5	15.00	65.00	45.00	42.80	19.08
Solea solea	5	11.00	51.00	24.60	29.80	16.33
Sprattus sprattus	5	5.10	14.00	9.70	9.56	3.65
Trachurus trachurus	5	6.10	39.40	20.50	22.26	13.02
Trisopterus luscus	5	10.00	32.00	20.00	20.52	8.47
Zeus faber	4	10.00	47.00	28.00	28.25	15.65

The three-dimensional models, the extracted metrics, and the metadata associated with the species are available in the SEANOE database [16], where the script for the automatic extraction of morphometric parameters is also accessible.

For each individual, the total length of the fish (TL, cm) was measured from the tip of the snout to the end of the caudal fin. The following metrics were extracted for each otolith: OL (mm) length, OW (mm) width, OH (mm) height (**Figure 1**), OA (mm^2) projected area, and OV (mm^3) total volume.

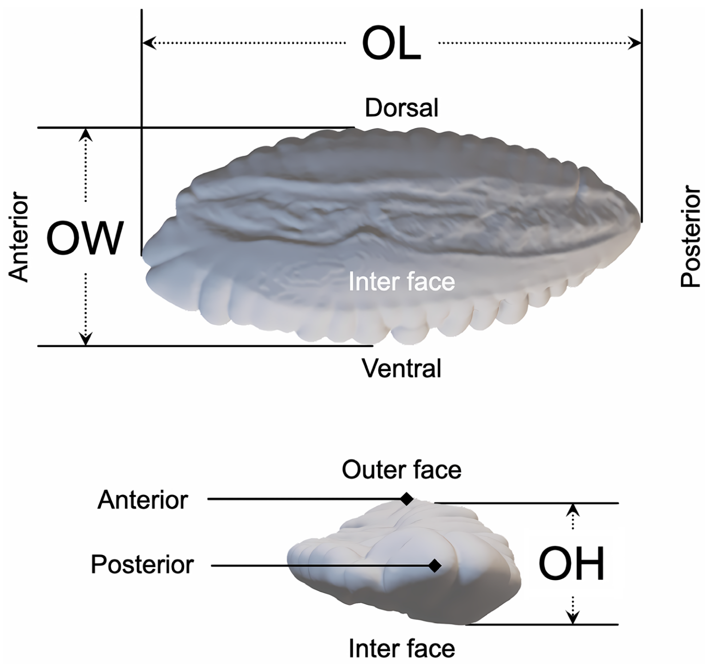

Figure 1. Otolith length (OL), width (OW) and height (OH) of *Gadus morhua*.

2.2. Statistical Analysis

The relationship between body size and various otolith metrics was assessed using a log-linear allometric model (Equation (1)):

$$\ln(\mathrm{TL}) = a + b \times \ln(x) \tag{1}$$

where x corresponds to the metric considered (OL, OW, OH, OA or OV), a is the ordinate at the origin and b is the allometry coefficient. In addition, the internal relationship between otolith length (OL), otolith width (OW) and otolith volume (OV) were also examined using this same log-linear allometric regression. This approach aimed to assess the extent to which otolith length, commonly used as an indicator of otolith size, serves as a reliable proxy for actual otolith volume [5].

Logarithmic transformation is traditionally used to quantify allometric growth relationships in fish and their calcified structures [7] [17] [18]. This transformation stabilizes variance and linearizes the exponential relationship between otolith dimensions and fish size [19]. After adjustment, the predicted values were back-transformed to the original scale by exponentiation in order to represent the relationships as exponential curves. The goodness-of-fit of the models was evaluated using the coefficient of determination (R^2), which measures the proportion of explained variance, and the overall Fisher test (F-statistic), whose p-value assesses the significance of the relationship [5] [6]. All analyses were performed in R [20].

3. Results

The relationships between total fish length (TL) and the various otolith metrics (OL, OW, OH, OA, and OV) are all significant ($p < 0.001$), indicating positive allometric growth of the otoliths relative to body size (Figure 2).

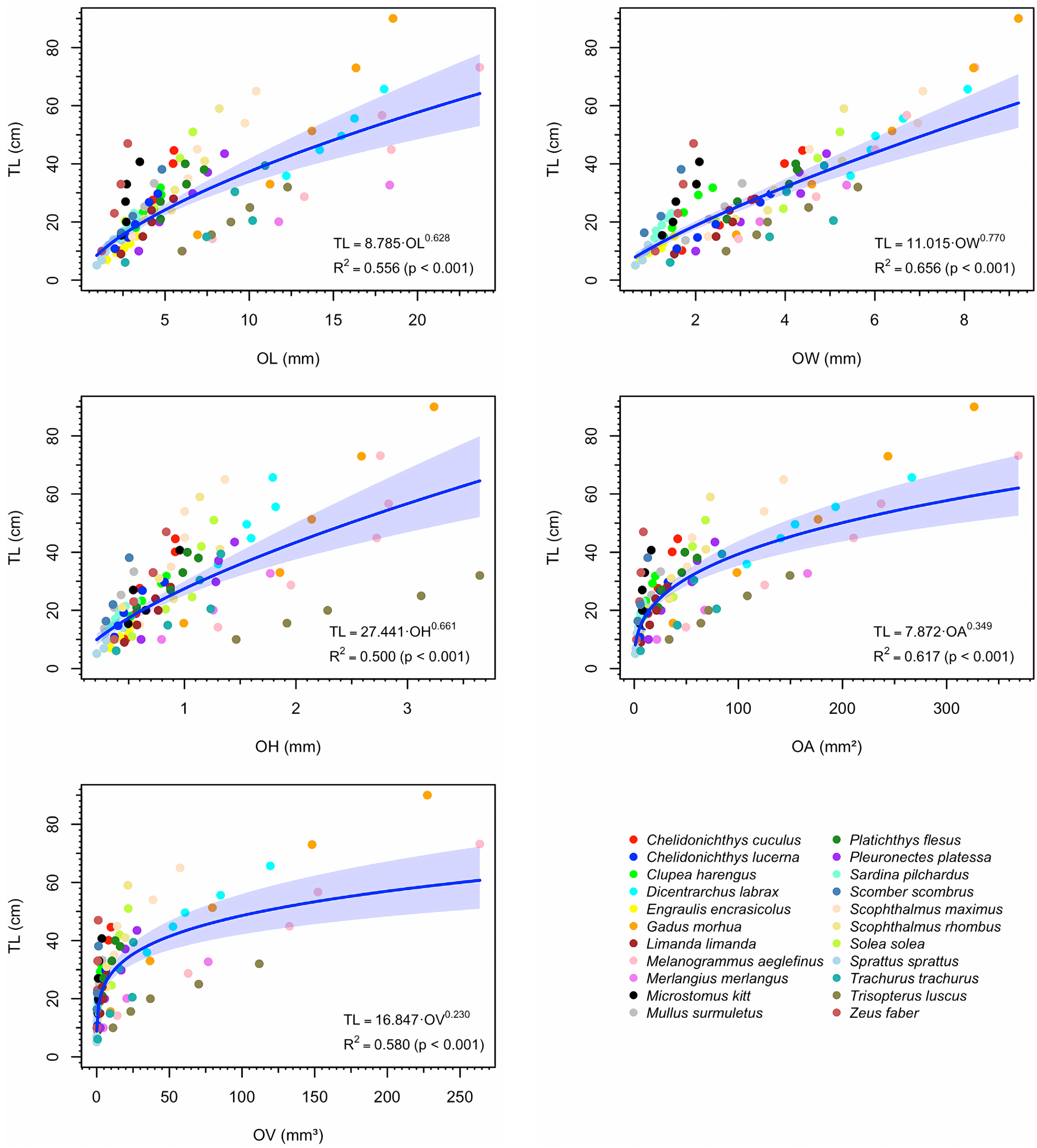

Figure 2. Relationships between Total Length (TL) and otolith metrics: length (OL), width (OW), height (OH), area (OA) and volume (OV). The blue curves represent exponential fits, with coefficients of determination (R^2) and significance ($p < 0.001$). The colour of each point represents fish species.

Otolith length (OL) shows a moderate correlation with total fish length (R^2 = 0.556), while width (OW) displays the strongest observed correlation (R^2 = 0.656). Height (OH) exhibits the weakest relationship (R^2 = 0.500), suggesting greater variability of this parameter among individuals and species. For a fish of a given size, the height of the otolith varies greatly from one species to another. Furthermore, for demersal fish (*e.g.*, pouting, *Trisopterus luscus*), the otolith is larger than that of pelagic and benthic fish (**Figure 2**).

Three-dimensional metrics also show significant relationships with body size. The R^2 value of Area parameter (OA) was 0.617. This value is higher than this volume parameter (OV, R^2 = 0.580) (**Figure 2**). These two 3D parameters are therefore comparable, or slightly superior, to linear metrics in terms of predictive power.

Overall, the general trend indicates an exponential increase in otolith dimensions with body size, consistent with an allometric growth model. This relationship suggests that, while all metrics are good indicators of fish size, width (OW) and area (OA) are the best predictors among those tested.

The relationship between otolith length (OL) and otolith volume (OV) was highly significant, revealing a clear allometric pattern. The log-linear model showed a strong fit, with a coefficient of determination R^2 = 0.943 (p-value < 0.001). The relationship between otolith width (OW) and otolith volume (OV) was also very high, R^2 = 0.937 (p-value < 0.001).

When analysed at the species level, the predictive accuracy of the otolith–fish size relationships was generally high, with coefficients of determination (R^2) averaging around 0.950 for most species. This indicates that, in the majority of cases, otolith morphometric metrics provide a strong estimate of fish total length. However, specific comparisons such as the lower predictive performance noted for the brill (*Scophthalmus rhombus*, R^2 = 0.848) must be viewed as indicative rather than definitive with sample sizes restricted to 3 - 5 individuals. These regression models lack the statistical power to reliably identify true inter-specific differences in allometric precision.

4. Discussion

The results suggest the robustness of allometric relationships between body size and otolith dimensions, in agreement with numerous previous studies [5]-[7] [17] [21]. These relationships rely on the fact that otolith growth is generally more stable and less influenced by short-term environmental variations than somatic growth, making otoliths reliable indicators of individual size and age [2] [22]. However, the nature of these relationships whether isometric or allometric varies depending on species, ontogenetic stage, and environmental conditions [23] [24]. While some studies have reported linear (isometric) relationships between fish length and otolith dimensions [25], others have documented negative allometric growth for otolith length and height, and positive allometry for otolith weight [24], indicating that otolith weight may accumulate relatively faster than body length during ontogeny. These variations underscore the importance of species-specific calibration when using otoliths for size reconstruction in ecological and paleoecological studies.

Contrary to our initial hypothesis, the simple one-dimensional metric of otolith width (OW) demonstrated the strongest correlation with body length (TL) in the multi-species model ($R^2 = 0.656$), slightly outperforming the integrative three-dimensional metrics of area ($R^2 = 0.617$) and volume ($R^2 = 0.580$). This suggests that for generalized multi-species models, the added complexity of 3D extraction may not always yield better statistical precision than robust 1D measurements. However, it should also be noted that the estimate based on otolith length (OL) was lower than the estimate based on three-dimensional metrics. This performance can be attributed to their integrative nature. Unlike simple linear measurements such as length (OL), width (OW), or height (OH), these variables capture the volumetric growth of the otolith and thus more accurately reflect overall variations in body size [26]. The use of such three-dimensional metrics therefore appears particularly relevant when estimating fish size from isolated or fragmented otoliths, especially when linear dimensions cannot be reliably measured [21] [27]. However, otolith width (OW) also demonstrated a very high correlation with fish length, consistent with findings from previous studies on various teleost species. Similar strong relationships between OW and fish size have been documented in mesopelagic fishes from the Mediterranean Sea [6] and in *Sardinella sindensis* from the Persian Gulf, where correlations between fish length and otolith dimensions were all significant, with R^2 values ranging from 0.73 to 0.87 [25]. This suggests that while volumetric parameters offer theoretical advantages, traditional linear measurements, particularly width, remain robust predictors of fish size across diverse taxa and environmental contexts [19]. The superior performance of otolith width (OW) in this multi-species context suggests it offers a cost-effective alternative to 3D processing, striking an optimal balance between precision and throughput for large-scale ecological or archaeological studies. However, this apparent stability may be an artifact of pooling morphologically distinct taxa, such as flatfish and roundfish, potentially masking inter-specific inconsistencies. As evidenced by the lower predictive power for *Scophthalmus rhombus*, a one-size-fits-all approach requires rigorous species-specific validation with larger sample sizes ($n > 5$). Furthermore, single linear dimensions fail to capture the decoupling of somatic and otolith growth [22] [27], particularly thickness accretion during metabolic suppression, nuances that only three-dimensional data can resolve for older, slow-growing individuals.

Traditionally, most studies examining otolith-fish relationships have relied primarily on otolith length as the main morphometric descriptor of growth [1] [19] [28]. Otolith length is often used as a proxy for otolith volume, based on the assumption of an approximately isometric relationship between linear and volumetric growth [5] [6]. In the present study, otolith length explains nearly 95% of the variation in otolith volume, supporting the validity of this approximation for many practical applications. The positive allometric coefficient reflects the non-linear, three-dimensional expansion of otoliths, in which growth occurs not only along the main axis but also through increased surface complexity and depth [7] [29]. Such 3D growth dynamics highlight that volumetric parameters provide a more integrative and biologically meaningful representation of otolith development than linear dimensions alone [10] [11].

Although otolith length remains a useful proxy, direct volumetric measurements capture the structural complexity of otolith accretion more accurately, offering enhanced precision for studies of growth, species discrimination, and environmental reconstruction. However, this simplification may overlook subtle but ecologically meaningful variations in otolith shape and density that are better captured by three-dimensional metrics [30] [31]. Recent advances in micro-CT imaging and 3D morphometrics now enable direct quantification of otolith volume and three-dimensional shape features, providing a more comprehensive and potentially more accurate measure of growth [16]. Using otolith volume rather than a linear proxy may therefore improve estimates of fish size and growth dynamics, especially in comparative or multi-species contexts where otolith shape varies substantially among species [32] [33].

An important aspect of this study lies in the fact that it combines data from multiple species with differing life histories, habitats, and growth strategies within the same ecosystem. This biological diversity introduces interspecific variability that may reduce the strength of the observed correlations. Otolith growth is strongly influenced by ecological behaviour, notably, the results indicated that demersal species (*e.g.*, *Trisopterus luscus*) possess relatively larger otoliths than pelagic or benthic species. This is consistent with the hypothesis that fish inhabiting dimmer, structurally complex demersal environments may require larger otoliths to facilitate enhanced hearing sensitivity and vestibular perception compared to their pelagic or benthic counterparts [7]. Environmental factors including depth, water temperature, and substrate type also contribute to variations in otolith morphology and size relationships [7] [32]. Consequently, the allometric coefficients estimated in this study should be interpreted as average trends that incorporate a high degree of interspecific variability. Species-specific calibrations would therefore be necessary to refine these relationships and improve the accuracy of size estimations, particularly for ecological and paleontological applications where precise reconstructions are required [5] [6].

The relatively lower values of predictive accuracy observed for certain otolith–fish size relationships may reflect species-specific differences in otolith shape and growth dynamics, or could be influenced by the limited sample size available for some taxa. Indeed, for most species, only 3 to 5 individuals were analysed, which restricts the statistical robustness of the model fits and the ability to detect subtle ontogenetic or ecological effects. Small sample sizes are particularly limiting when attempting to characterize the full range of size-related allometric variation or to account for intraspecific variability due to sex, age class, or environmental conditions [17]. Therefore, these results must be interpreted with extreme caution. The sample sizes (from 3 to 5 per species) are insufficient to establish stable species-specific predictive equations, and the resulting wide confidence intervals mean that any apparent differences in predictive performance between species are likely artifacts of sampling rather than biological reality. The current results should be interpreted as identifying broad allometric trends rather than definitive species-specific rules. Future studies must increase sampling density to statistically validate these hierarchy of metrics and refine species-specific growth models. Nonetheless, the generally high precision across species ($R^2 > 0.80$ for most relationships) suggests that the overall allometric pattern between otolith and fish size remains consistent despite limited sampling, supporting the use of generalized multi-species models for preliminary size estimations when species-specific data are unavailable.

Certain limitations must also be acknowledged. The relationship between fish size and otolith size can vary among species and ontogenetic stages, warranting the development of species-specific or hierarchical models to account for such variability [11]. Moreover, environmental factors such as temperature, salinity, and food availability may differentially affect somatic and otolith growth, leading to decoupling between these two parameters under certain physiological or ecological conditions [34] [35]. This phenomenon has been documented in situations of prolonged starvation, metabolic stress, or exposure to suboptimal thermal regimes, where otolith deposition may continue despite reduced or arrested somatic growth [22]. Such decoupling can introduce bias into back-calculation methods and size estimation models, particularly when applied across diverse environmental contexts or life stages.

The relationships identified in this work have important implications across several research domains. In trophic ecology, they allow for more accurate estimation of prey size consumed by piscivorous predators, thereby contributing to a better understanding of trophic interactions, energy flow, and size-selective predation within marine ecosystems [5] [21]. In archaeology and palaeoecology, linking otolith morphometry to body size provides a reliable and non-destructive tool for reconstructing past fish population size structures, fishing pressure, and inferred historical environmental conditions based on assemblages recovered from sedimentary deposits or archaeological middens [17] [27]. In fisheries science, these relationships offer an effective and time-efficient approach for estimating fish size when only otoliths are available, such as in the analysis of predator stomach contents, sedimentary remains, or fisheries by-catch and discards [6].

Moreover, this study suggested the widely accepted notion that otolith length serves as a significant proxy for the overall three-dimensional structure of otoliths. The strong correlation between otolith length and volume validates the continued use of linear measurements in studies where volumetric data are unavailable, while also highlighting the added value of 3D imaging techniques when greater morphometric precision is required [16]. This dual finding supports a strategic approach to method selection. It indicates that 2D measurements, particularly width, are best suited for large-scale, routine fisheries analyses where speed and cost-efficiency are essential, whereas 3D methods are preferable for paleoecological studies with fragmented otoliths or for research requiring maximal morphological precision to detect subtle shape variations.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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