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A window into the ghost shark's life: eye lenses reveal a biphasic trophic strategy driven by neonatal generalism

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ABSTRACT

Holocephalans, or ghost sharks, are ecologically significant but poorly understood cartilaginous fishes facing intense yet poorly quantified pressure from fisheries. Effective management is hindered by a critical knowledge gap: the continuous, lifetime trophic development of individuals remains uncharacterized. While conventional methods provide dietary snapshots, an individual's complete life-history strategy has remained elusive. Here we tested the hypothesis that the plownose chimaera (*Callorhinchus callorynchus*) undergoes predictable ontogenetic shifts in its isotopic trophic niche and habitat use. We present the first continuous reconstruction of a holocephalan's life history by analyzing the isotopic archive preserved within concentric layers of the eye lens. Our analysis reveals a complex, biphasic trophic strategy. Counterintuitively, neonates exhibit an exceptionally broad, generalist isotopic niche, a likely strategy to minimize competition with adults during a vulnerable stage. This niche contracts sharply after the first year, marking an abrupt transition to a more specialized foraging strategy. Subsequently, individuals undergo a gradual, lifelong increase in trophic position and a systematic shift toward more pelagic habitats, culminating in a decoupled niche expansion where adults broaden their foraging habitat without altering their core trophic level. These findings deliver a quantitative framework for the ecosystem-based management of this and other data-poor species. By identifying distinct nursery habitats and clarifying the shifting ecological role of the adult population, our work provides the detailed biological information necessary to advance conservation strategies.

1. Introduction

Cartilaginous fishes are a monophyletic, diverse, and ancient lineage including two sister taxa, the Elasmobranchii (i.e. sharks and rays) and the enigmatic Holocephali (i.e. chimaeras or ghost sharks) (Grogan et al., 2012). Many of them occupy crucial ecological niches, especially as meso-benthic predators structuring seafloor communities (Canales-Cerro et al., 2022). Such is the case of the holocephalans are exceptionally vulnerable to intensive fishing pressure, a pervasive threat shared by many chondrichthyan lineages (Finucci et al., 2020; Dulvy et al., 2026). This susceptibility underscores the urgent requirement to characterize their biology, ecology, and population dynamics (Dulvy et al., 2024). Along the coasts of the south eastern Pacific and the south western Atlantic, for instance, the plownose chimaera (*Callorhinchus callorynchus*) has been frequently caught by artisanal fishing (Hernández et al., 2010; Bernasconi et al., 2015). Beyond direct fishing mortality as target and non target species, plownose chimaeras are exposed to complex physiological and ecological stressors. Furthermore, the identification of persistent organic pollutants in *C. callorynchus* by Chierichetti et al. (2017) underscores both its exposure to chemical contamination and its potential as a bioindicator of marine ecosystem health. These coastal regions likely function as seasonal feeding grounds

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for the species (Chierichetti et al., 2021). Therefore, advancing our knowledge of the biology and ecology of key species, such as the plownose chimaera, is essential in designing effective conservation and management strategies to secure the future of these unique populations (Erk et al., 2025). Altogether, these reports reveal a complex threat landscape where the interplay of overfishing, habitat degradation, and pollution defines the cumulative risk to these enigmatic species (Chierichetti et al., 2021).

Our understanding of holocephalan trophic ecology has advanced significantly, establishing their fundamental role as benthic predators in diverse marine ecosystems (Pethybridge et al., 2011; Dedman et al., 2024). Foundational research focused on describing the dietary composition of key species such as the plownose chimaera, *Callorhinchus callorynchus*, in Patagonian waters off the south western Atlantic (Di Giácomo and Perier, 1996) remains active and has since expanded geographically to the south eastern Pacific, aiming to elucidate local and regional dietary variations (Canales-Cerro et al., 2022; Román et al., 2020).

Contemporary research now integrates multiple methodologies, combining traditional stomach content analysis with biochemical tracers such as fatty acids and stable isotopes (Young et al., 2022). This approach yields a higher-resolution characterization of diet and trophic position (Pethybridge et al., 2011; Silva-Garay et al., 2018). These modern techniques have revealed complex ecological dynamics, including ontogenetic dietary shifts as individuals mature (Moura et al., 2005) and niche segregation mechanisms that permit coexistence with other demersal chondrichthyans (Albo-Puigserver et al., 2015; Dunn et al., 2010b). Ultimately, the precise characterization of their feeding ecology is critical; since it not only defines their functional role within benthic food webs (Arrighetti et al., 2018), but also provides the bio-ecological data essential for developing effective conservation strategies for these often rare and poorly understood fishes (Mulas et al., 2021).

Trophic ecology defines the energy flow through ecosystems and determines the functional role of species, a concept that forms a cornerstone of Fishery Science, Ecology and Conservation biology (Garvey and Whiles, 2016). For commercially exploited fish species, the study of diet is no mere academic exercise; it provides the essential scientific foundation for developing the ecosystem models and management strategies required for long-term sustainability. Within this field, stable isotope analysis of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) offers substantial advantages over traditional methods like stomach content analysis. Whereas stomach contents reveal only the most recent meal, stable isotopes integrate an organism's diet over weeks to months, providing a long-term perspective on the resources actually assimilated into its tissues (Fry, 2006; Michener and Lajtha, 2007). This technique also enables the tracing of nutrient origins and the tracking of animal migrations across distinct isotopic landscapes (isoscapes) (Alexandre, 2020). Therefore, the synergistic combination of these methods represents the most robust approach. Stomach content analysis provides taxonomic identification of ingested prey, while isotope ecology quantifies its assimilated contribution to the predator's diet, yielding a truly comprehensive understanding of trophic interactions.

The fish eye lens is an exceptional natural archive that provides a high-resolution record of an individual's life history, data fundamental to modern fisheries management. Unlike metabolically active tissues, the eye lens grows through the sequential addition of concentric layers and is metabolically inert. This unique combination of properties ensures the preservation of a continuous chronological record of a fish's dietary isotopic signature (Tzadik et al., 2017; Wallace et al., 2014). Microanalysis of these layers enables the reconstruction of ontogenetic shifts in diet and habitat use with remarkable precision, from juvenile stages to adulthood (Faletti and Stallings, 2021; Kurth et al., 2019; Young et al., 2022). This technique has been applied to decipher the migratory histories and population structure of high-value commercial species such as the jumbo squid (*Dosidicus gigas*) (Liu et al., 2020) and to determine the spawning origins of demersal fishes (Vecchio and Peebles, 2020). Furthermore, radiocarbon (^{14}C) analysis of the lens core has revolutionized age validation, revealing centuries-long lifespans in species like the Greenland shark (Nielsen et al., 2016) and confirming age estimates for reef fish (Patterson et al., 2021). The eye lens is therefore not merely a complement to otoliths but an indispensable tool for species lacking calcified ageing structures, particularly elasmobranchs (Quaeck-Davies et al., 2018; Simpson et al., 2019). These biological archives—integrating continuous individual growth trajectories and ontogenetic habitat shifts—underpin robust stock assessments. Such high-resolution life-history records refine the parameterization of age-structured models and delineate critical nursery habitats, thereby reducing the uncertainty inherent in conventional assessments and facilitating ecosystem-based management.

Despite research into the population-level biology of the plownose chimaera, such as its growth and maturity is already in place (Alarcón et al., 2015), a critical gap in our understanding of its individual trophic life history still remains. Previous studies on related species have described ontogenetic dietary shifts using stomach contents from different sizes (Dunn et al., 2010a; Moura et al., 2005). Precise characterization of feeding ecology is essential to defining the functional roles of holocephalans within benthic food webs. These high-resolution data underpin the development of targeted conservation strategies for such data-deficient species. Our study aims to fill that gap by using sequential stable isotope analysis ($\delta^{13}C$) and ($\delta^{15}N$) of the eye lens to reconstruct the trophic ecology of *C. callorynchus* throughout its life in south eastern Pacific waters. We hypothesize that an individual's trophic niche and habitat use evolve predictably with its developmental stage, and that these changes are permanently recorded in the isotopic composition of the lens. To test this hypothesis, we will analyze nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotope signatures across the concentric laminae of the lens—from the core (juvenile stage) to the periphery (adult stage)—as proxies for trophic position and foraging habitat, respectively. Based on this hypothesis, we predict that (1) $\delta^{15}N$ values will exhibit progressive enrichment toward the outer layers, reflecting an increasing trophic position as individuals grow and consume larger prey; (2) $\delta^{13}C$ values will show a consistent directional shift, indicating systematic changes in foraging habitat (e.g., from coastal to deeper zones) during ontogeny and, (3) isotopic variance for both $\delta^{15}N$ and $\delta^{13}C$ will be greater in the outer layers than in the core, indicating a trophic niche expansion and a more generalist diet in adults.

2. Methods

2.1. Sample collection and processing

A total of 28 plownose chimaera, with a mean total length of 74.6 ± 9.43 cm, were collected from artisanal midwater trawls at depths of 20–40 m in Valparaiso Bay, Caleta Higuerillas and Caleta Montemar in 2023 (Fig. 1a). Following capture, all specimens were immediately frozen at −20 °C. In the laboratory, the left eye of each individual was excised and processed following established protocols (Bell-Tilcock et al., 2020). Briefly, lenses were thawed and moistened with deionized water, and the intact lens diameter was measured using an Olympus SZX16 dissecting microscope (20× magnification) equipped with an Axiocam 208 color camera (ZEISS). Subsequently, six to seven outer layers (laminae) were sequentially peeled from each lens using fine-tipped forceps. The core was defined as the dense, central portion remaining once the lens diameter was reduced to <500 μm, which resisted further delamination (Fig. 1b).

2.2. Stable isotope analysis

The separated laminae and the core from each lens were placed in individual tin capsules, dried for 12 h, and weighed for stable isotope analysis (SIA). Isotope ratios of nitrogen $\delta^{15}N$ and carbon $\delta^{13}C$ were

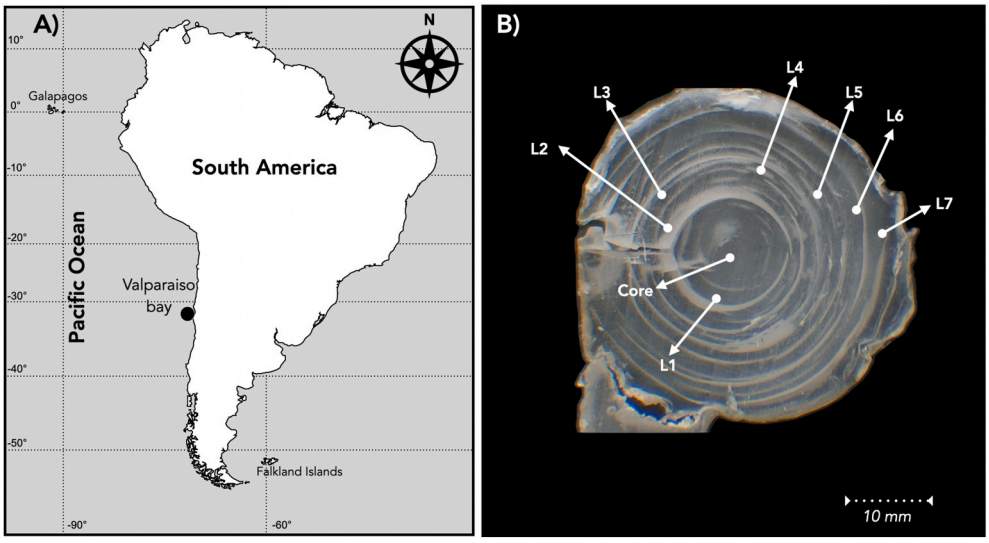


Fig. 1. A) Location of Valparaíso Bay, Chile, in the southeastern Pacific Ocean, where plownose chimaera (*Callorhinchus callorynchus)* specimens were collected. B) Cross-section of a *C. callorynchus* lens showing the core and six laminae analyzed in this study. The scale bar represents 10 mm.

determined at the Stable Isotope Facility (LAI) of Universidad Andres Bello. Analyses were performed using a Eurovector EA-3024 elemental analyzer coupled to a Nu-Instruments continuous-flow mass spectrometer. Isotope ratios are reported in standard delta (δ) notation in parts per thousand (‰), where δ = [(R sample/Rstandard) – 1]. The term R represents the ratio of heavy to light isotopes ($^{13}C/^{12}C$ or $^{15}N/^{14}N$). Values were calibrated against Vienna Pee Dee Belemnite (VPDB) for $\delta^{13}C$ and atmospheric N_2 for $\delta^{15}N$. Analytical precision, based on repeated measures of certified standards, was ±0.1‰ for both $\delta^{15}N$ and $\delta^{13}C$.

2.3. Data analysis

We quantified the isotopic niche breadth and structure using a suite of metrics derived from the geometric distribution of individuals in δ-space (Layman et al., 2007). To contextualize habitat use, we established $\delta^{13}C$ and $\delta^{15}N$ baselines using two sympatric species representing distinct energy pathways: the porcelain crab *Petrolisthes granulosus* (benthic) and the red squat lobster *Grimothea monodon* (pelagic-influenced) (Canales-Cerro et al., 2022). We selected these primary consumers because their stable isotopic signatures integrate the localized carbon and nitrogen baselines of the Valparaíso Bay ecosystem. All metrics were calculated in R using the 'SIBER' package (Jackson et al., 2011). Key metrics included the total convex hull area (TA), representing the full extent of the isotopic niche; the $\delta^{13}C$ range (CR) and $\delta^{15}N$ range (NR), which serve as proxies for niche width along the habitat and trophic position (TP) axes, respectively; and the standard ellipse area corrected for sample size (SEAc), which estimates the core isotopic niche. The shape and orientation of this core niche were further characterized by calculating its eccentricity (E) and major angle (θ). The TP was calculated by:

1) $\delta^{15}N_c = \Delta N\ (TP + \lambda) + \alpha\ (\delta^{15}N_{b1} + \delta^{15}N_{b2})$ - $\delta^{15}N_{b2}$ and,
2) $\alpha = ((\delta^{13}C_{b2} - (\delta^{13}C_c + \Delta C))/(TP - \lambda)/(\delta^{13}C_{b2} + \delta^{13}C_{b1})$

Where the subscript C denotes the consumer (plownose chimaera) and b denotes the isotopic baseline. The two baselines used in the model were baseline 1 (b_1), represented by the crab *Petrolisthes granulosus* ($\delta^{13}C = -15.09 \pm 0.54$‰ - $\delta^{15}N = 14.25 \pm 1.22$‰), and baseline 2 ($b_2$), represented by the red squat lobster *Grimothea monodon* ($\delta^{13}C = -15.52 \pm 0.12$‰ - $\delta^{15}N = 17.56 \pm 1.23$‰) (Canales-Cerro et al., 2022). We applied trophic discrimination Factors (TDFs; ΔN and ΔC) from McCutchan et al. (2003), with a ΔN of 2.9 ± 0.32‰ and a ΔC of 1.3 ± 0.30‰. The parameter λ represents the trophic position of the baselines, and α is the proportion of nitrogen in the consumer derived from baseline 1. Accurate TP estimation in ecosystems with multiple basal resources, such as distinct pelagic and benthic food webs, requires a method that can discriminate between these energy sources. To address this, we employed a two-baseline model for TP calculation. This equation is specifically designed for such systems, as it incorporates the $\delta^{13}C$ and $\delta^{15}N$ values of both baselines and includes a mixing parameter α, which represents the proportional contribution of nitrogen derived from the primary baseline. By integrating $\delta^{13}C$ data to correctly partition the nitrogen sources, this approach provides a more robust and ecologically realistic TP estimation than single-baseline models (Quezada-Romegialli et al., 2018).

To test the hypothesis that trophic niche and habitat use evolve with ontogeny, we used a hierarchical statistical approach that accounted for the nested structure of our data (i.e., multiple eye lens layers within each individual). Initial visualization of individual isotopic trajectories for both $\delta^{15}N$ and $\delta^{13}C$ revealed generally linear trends and quantifiable inter-individual variability, supporting the application of linear models. We fitted separate linear mixed models (LMMs) for the $\delta^{15}N$ and $\delta^{13}C$ datasets, with layer position included as a continuous fixed effect. This framework allowed us to test our primary predictions by estimating the average population trend (the fixed effect) while simultaneously modeling individual-specific variation in initial isotopic values (random intercepts) and their rates of change over time (random slopes). Within the $\delta^{15}N$ model, a positive and significant slope was interpreted as an increase in trophic position (Prediction 1). For the $\delta^{13}C$ model, a slope significantly different from zero indicated a systematic shift in foraging habitat (Prediction 2). To test our third prediction of trophic niche expansion, we used a Levene's test to formally compare the isotopic variance between the innermost (core) and outermost layers of the lens. The assumptions of all models were validated via residual analysis to ensure the robustness of our statistical inferences.

3. Results

From the 28 individuals sampled, a total of 211 eye lens laminae and cores were analyzed (Table 1). The number of laminae per individual ranged from zero (core only) to seven. $\delta^{13}C$ values ranged from −18.6‰ to −9.6‰, with a mean of −15.2 ± 1.5‰. The full range of values spanned signatures consistent with both pelagic (approx. −18‰) and

Table 1
Stable isotope composition of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), carbon-nitrogen ratio (C:N), and trophic position (TP) for the core and the seven sequential laminae analyzed of the plownose chimaera in the south eastern Pacific waters. Data are presented as the mean followed by the standard deviation (sd) in parentheses. *n* indicates the number of subsamples analyzed for each layer.

Laminae	$\delta^{13}C$ (sd)	$\delta^{15}N$ (sd)	C:N (sd)	TP (α)	*n*
Core	−13.34 (1.89)	6.4 (2.18)	3.41 (1.05)	2.79 (0.59)	29
Laminae 1	−14.90 (1.15)	7.75 (1.53)	3.39 (0.59)	3.25 (1.79)	29
Laminae 2	−15.60 (1.21)	7.74 (1.34)	3.57 (0.45)	3.23 (0.76)	29
Laminae 3	−15.77 (1.06)	8.07 (1.56)	3.47 (0.54)	3.36 (1.21)	29
Laminae 4	−15.73 (1.20)	8.32 (2.26)	3.72 (1.26)	3.22 (1.49)	29
Laminae 5	−15.55 (0.95)	8.18 (1.95)	3.50 (0.42)	3.36 (2.58)	28
Laminae 6	−15.47 (1.06)	8.88 (1.82)	3.51 (0.27)	3.61 (0.98)	25
Laminae 7	−15.28 (1.12)	8.81 (2.11)	3.47 (0.45)	3.57 (0.86)	13

more enriched benthic/coastal (approx. −10‰) carbon sources. $\delta^{15}N$ values varied widely, from 2.3‰ to 16.8‰ (mean = 7.9 ± 2.0‰). This 14.5‰ range corresponds to approximately four trophic levels, assuming a per-trophic-level enrichment factor of 2.9‰ (McCutchan et al., 2003). Elemental analysis revealed a mean carbon content of 47.3 ± 6.4% (range: 7.4–69.8%) and a mean nitrogen content of 13.7 ± 2.0% (range: 4.6–26.0%). The resulting mean C:N ratio of approximately 3.4 falls within the expected range for non-lipid-rich marine vertebrate tissues, confirming high sample quality and analytical integrity (Layman et al., 2007; Logan et al., 2008). The biplot reveals a distinct two-phase ontogenetic shift in the trophic ecology of the plownose chimaera (Fig. 2). The first phase is a profound and abrupt transition occurring between the neonatal stage (core) and the first year of life (laminae 1). Neonates occupy a highly restricted and isotopically distinct niche, separate from all subsequent laminae. The second phase, from laminae 1 to laminae 7, is characterized by a gradual and continuous trophic development. During this period, individuals exhibit a progressive increase in $\delta^{15}N$ alongside a directional shift in $\delta^{13}C$ values. The gradual nature of this secondary shift is evidenced by the substantial overlap in isotopic niche space between consecutive laminae classes.

Our analysis revealed a significant positive linear relationship between laminae and TP, supporting our first prediction. The linear mixed model identified laminae as a strong positive predictor of TP (slope (β_1) = 0.089, $p < 0.001$). The fixed-effect component of the model, described by the equation TP = 2.988 + 0.089 × laminae, indicates that an individual's trophic position increases by approximately 0.09 levels per laminae. This positive trend is further illustrated by the narrow 95% confidence intervals around the regression slope (Fig. 3a). While the population-level trend was clear, we also observed considerable inter-individual variability in TP at any given laminae. The random effects component of the LMM quantified this variation, confirming that individuals differed significantly in both their initial TP at the core and their rate of trophic increase over their lifetime. Consistent with our second prediction, our analysis revealed a significant, negative linear relationship between laminae and $\delta^{13}C$ signatures. The LMM demonstrated a progressive decline in $\delta^{13}C$ values with layer, with a mean β_1 of −0.244‰ per laminae ($p < 0.001$). This systematic $\delta^{13}C$ depletion indicates a clear ontogenetic shift in foraging habitat, moving from coastal or benthic ecosystems with enriched carbon sources toward more pelagic environments that rely on a depleted carbon base. This ontogenetic shift reflects a transition from pelagic-influenced foraging—supported by a $\delta^{13}C$-depleted carbon base—toward more $\delta^{13}C$-enriched benthic food webs. While this population-level trend was strong, we also observed considerable isotopic variability within each laminae suggesting significant inter-individual differences in foraging strategies (Fig. 3b).

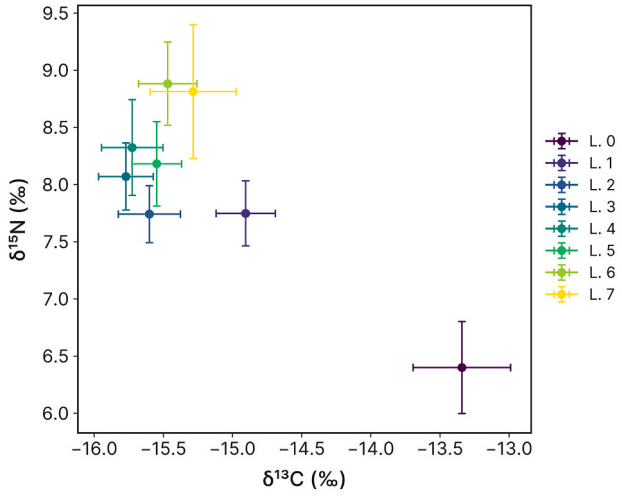


Fig. 2. Bi-plot isotopic niche space of the plownose chimaera (*Callorhinchus callorynchus*) based on stable isotope analysis. The plot shows the mean carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values for each laminae (0–7). Error bars represent the standard deviation for each isotope. The number of individuals (n) analyzed in each group is indicated in the legend.

Our findings reveal a decoupled expansion of the isotopic niche, where the breadth of foraging habitat increases with laminae while trophic niche width remains stable, thus only partially supporting our third prediction (Fig. 4). Analysis of the $\delta^{13}C$ showed a statistically significant increase in variance from the lens core to the outer layers (Levene's Test, $p = 0.013$). This isotopic dispersion indicates that adults utilize a broader range of carbon sources than juveniles, consistent with a horizontal expansion of their foraging niche. In stark contrast, the variance of the $\delta^{15}N$, which reflects trophic level breadth, did not differ significantly between early and late life stages ($p = 0.578$). This stability suggests that individuals maintain a consistent vertical trophic niche throughout their ontogeny. This decoupling reveals a sophisticated life-history strategy: individuals become more flexible in their foraging habitat without altering their fundamental trophic role. Such a pattern may act to minimize intraspecific competition between age cohorts, allowing adults to exploit a wider array of resources while maintaining their primary function within the food web.

Our life-history reconstruction of the plownose chimaera, using isotopic archives in the eye lens, reveals a complex biphasic development (Fig. 5). Initial neonatal generalism—spanning trophic positions from primary consumers to higher-order levels—undergoes a pronounced contraction after the first laminae. This transition marks a shift toward a more constrained isotopic niche, characterized by an elevated mean trophic position and a consistent reliance on ^{13}C-depleted carbon sources. With a total area of 34.36 $‰^2$ and a centroid distance of 2.59 (Table 2), the neonate niche far exceeds that of all other age classes, indicating that the youngest individuals exploit the widest range of habitats and resources. This early-life generalism spans from very low trophic levels to positions comparable to those of mature adults. This broad, generalist isotopic niche contracts sharply after the first year. The population transitions to a more restricted isotopic space characterized by a higher mean trophic position and a reliance on $\delta^{13}C$-depleted carbon sources, indicative of a shift to more pelagic foraging grounds. Following this foundational shift, from laminae 1 to 7, the isotopic niche size stabilizes, but individuals continue to track progressively higher trophic positions. This pattern suggests a phase of increasing specialization, where growing individuals become more effective predators on higher-value prey within an established habitat, leading to high isotopic overlap and potential intraspecific competition among older age classes. The pronounced isotopic breadth in neonatal cohorts likely reflects early-life foraging plasticity. However, this signature may also integrate maternal isotopic inheritance—representing the mother's pre-parturition nutritional investment—or the environmental heterogeneity typical of coastal nursery grounds. Subsequently, the systematic $\delta^{13}C$ depletion indicates a transition toward pelagic foraging. Although this

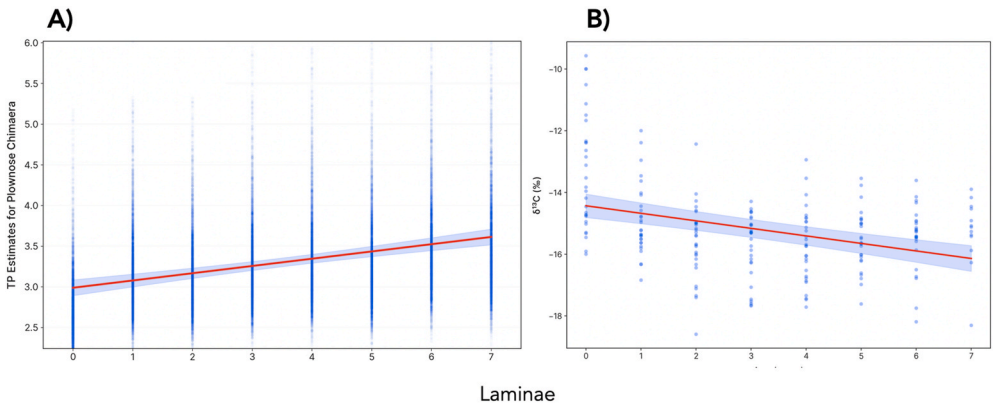


Fig. 3. Results of mixed linear models showing the relationship between laminae and key trophic metrics in the plownose chimaera (*Callorhinchus callorynchus*). A) The model for trophic position (TP) shows a significant positive trend with laminae. Individual points represent bootstrap estimates of TP = 2.988 + 0.089 x Laminae B) The model for carbon stable isotope values ($\delta^{13}C$) shows a significant negative trend with age. In both panels, the solid red line represents the fixed-effect regression, and the shaded blue area is the 95% confidence interval. Model equations and significance levels are provided on the plots. $\delta^{13}C = -14.43 - 0.244$ x Laminae. $\beta_1 = -0.244$, $p < 0.001$. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

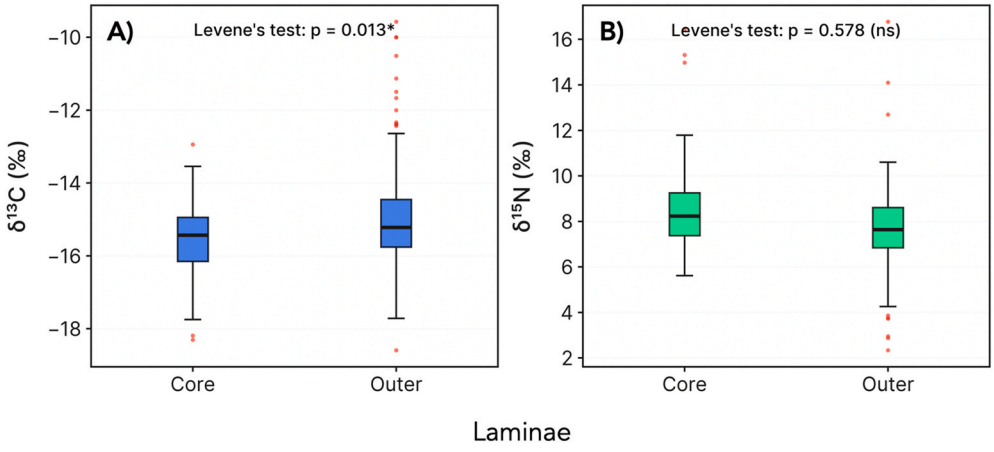


Fig. 4. Boxplots showing the distribution of A) $\delta^{13}C$ and B) $\delta^{15}N$ stable isotope values, comparing the Core and Outer layer groups. The central line in each box represents the median, box boundaries are the 25th and 75th percentiles, and whiskers extend to 1.5 times the interquartile range. Individual points are outliers. The results from Levene's test for homogeneity of variances are displayed for each isotope (* indicates $p < 0.05$; ns, non-significant).

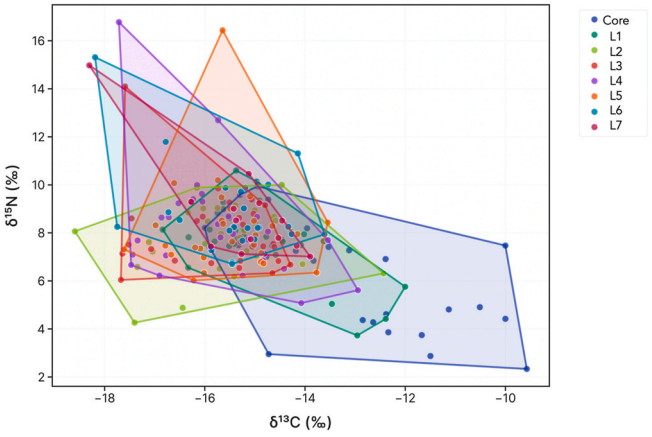


Fig. 5. Biplot of carbon ($\delta^{13}C$) versus nitrogen ($\delta^{15}N$) stable isotope values for the plownose chimaera (*Callorhinchus callorynchus*). Each point represents an individual, color-coded by laminae number as shown in the legend. The total area of the isotopic niche for each laminae is delineated by a corresponding colored convex hull. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Layman's metrics describing the point distribution in the core and the seven sequential laminae of the plownose chimaera. Reported are the total area (TA), the mean distance to the centroid (CD), and the mean nearest neighbor distance (NND). NND values are presented as the mean and standard deviation (sd) in parentheses.

Laminae	TA	CD	NND (sd)
Core	34.36	2.59	0.71 (0.56)
Laminae 1	16.15	1.51	0.47 (0.34)
Laminae 2	21.67	1.52	0.58 (0.40)
Laminae 3	16.26	1.56	0.53 (0.83)
Laminae 4	26.98	1.91	0.74 (0.90)
Laminae 5	23.39	1.59	0.66 (1.12)
Laminae 6	23.14	1.6	0.57 (0.84)
Laminae 7	9.87	1.63	1.02 (1.37)

interpretation aligns with established ontogenetic patterns in chimaeroids, $\delta^{13}C$ variability is also modulated by local productivity, seasonal fluctuations, and regional baseline shifts. Such confounding factors require careful consideration when reconstructing high-resolution habitat utilization from biochemical archives.

4. Discussion

Using the eye lens as a lifetime isotopic archive, we reveal a biphasic trophic strategy in the plownose chimaera (*Callorhinchus callorynchus*). Our results demonstrate a major trophic restructuring after the first year of life, transitioning from an broad neonatal isotopic niche to a more specialized adult foraging pattern. This initial shift is followed by a gradual, lifelong increase in trophic position and a progressive migration toward pelagic habitats. These findings provide the first continuous, individual-based reconstruction of this species' life history, uncovering a sophisticated ecological strategy that balances early-life generalism with adult specialization.

Our results largely support the central hypothesis that the trophic ecology of *C. callorynchus* shifts predictably across growth laminae. As predicted, we observed a progressive enrichment in $\delta^{15}N$ with the trophic position increasing by approximately 0.09 levels annually, confirming that individuals exploit higher-trophic-level prey as they grow. We also confirmed a systematic depletion in $\delta^{13}C$ values across laminae, indicating an ontogenetic habitat shift from coastal-benthic zones toward pelagic foraging grounds. Our third prediction, however, was only partially supported. While the variance in $\delta^{13}C$ increased with age—signifying an expansion of the horizontal foraging habitat—the variance in $\delta^{15}N$ remained constant. This decoupling reveals a nuanced strategy where adults expand their foraging range without altering their trophic breadth.

A key finding is this biphasic development, particularly the isotopic niche of neonates. This observation contrasts with typical ontogenetic patterns in many chondrichthyans, where juveniles often occupy a restricted niche to avoid predation and competition. We propose that early-life generalism is a critical survival strategy for *C. callorynchus*, allowing neonates to exploit diverse locally abundant resources during a vulnerable period, thereby minimizing competition with older conspecifics. This dynamic was previously undocumented, as prior studies relying on stomach content analysis provided only dietary snapshots (Di Giácomo and Perier, 1996; Román et al., 2020). The sharp contraction of the isotopic niche after the first year, coupled with the shift to pelagic habitats, marks a fundamental transition from juvenile opportunism to a defined adult foraging pattern. While the subsequent increase in trophic position and expansion of the $\delta^{13}C$ niche space aligns with other deep-water chimaeroids (Dunn et al., 2010b; Moura et al., 2005), the stable trophic breadth is a novel finding for this group. It suggests that while adults explore a wider geographic range, they maintain a specialized role as mesopredators, likely enhancing foraging efficiency while preserving their core function within the food web. Consequently, these lifetime reconstructions provide a critical ecological context that transcends the limitations of regional demographic and dietary studies (Alarcón et al., 2015; Canales-Cerro et al., 2022).

As a data-deficient species caught as both target and bycatch, the plownose chimaera presents a significant challenge for fisheries management (Finucci et al., 2020). First, identifying a distinct neonatal stage with specific habitat requirements underscores the need for spatial protections, such as conserving critical nursery areas. Second, understanding the adult shift toward pelagic habitats clarifies potential interactions with various fisheries and food web components. This high-resolution ecological data is crucial for developing effective bycatch reduction strategies and for accurately parameterizing food web models used to assess the ecosystem-level impacts of fishing (Dunlop et al., 2019). While this eye-lens-based approach offers an unparalleled lifelong perspective, we acknowledge certain limitations. Temporal resolution is constrained by the number of laminae that can be distinctly separated; thus, our age-based assignments represent yearly averages rather than fine-scale seasonal shifts. Furthermore, our interpretation of habitat use from $\delta^{13}C$ values relies on assumptions about coastal versus pelagic baselines, which may vary regionally. Finally, analyzing archived eye lens specimens provides a powerful tool for retrospectively reconstructing how this species has responded to historical changes in fishing pressure and climate.

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CRediT authorship contribution statement

Sebastian A. Klarian: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Ana B. Guzmán-Castellanos:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Writing – original draft, Writing – review & editing. **Francisco J. Concha:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – review & editing. **Juan Vargas-Perez:** Methodology, Software, Writing – review & editing. **Francisco Fernandoy:** Methodology, Software, Writing – review & editing. **Katherine Villa:** Conceptualization, Data curation, Methodology, Writing – review & editing. **Mauricio Hoyos-Padilla:** Conceptualization, Investigation, Visualization, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data plow nose (Original data).

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