Received: 6 August 2020 | Accepted: 28 November 2020

DOI: 10.1111/2041-210X.13543

PRACTICAL TOOLS

Methods in Ecology and Evolution BRITISH ECOLOGICAL SOCIETY

Advancing diet reconstruction in fish eye lenses

Miranda Bell-Tilcock[1] | Carson A. Jeffres[1] | Andrew L. Rypel[1,2] | Ted R. Sommer[3] | Jacob V. E. Katz[4] | George Whitman[1] | Rachel C. Johnson[1,5]

[1]Center for Watershed Sciences, University of California, Davis, CA, USA

[2]Department of Wildlife, Fish & Conservation Biology, University of California, Davis, CA, USA

[3]Department of Water Resources, West Sacramento, CA, USA

[4]CalTrout, San Francisco, CA, USA

[5]National Marine Fisheries Service, Southwest Fisheries Science Center, Santa Cruz, CA, USA

Correspondence
Miranda Bell-Tilcock
Email: mirbell@ucdavis.edu

Funding information
Department of Water Resources, Grant/Award Number: 4600011527; USBR, Grant/Award Number: R13PS20147

Handling Editor: Clive Trueman

Abstract

1. Tracking habitat use and dietary shifts in migratory species is vital to conservation and management. Yet, conventional animal tracking often precludes tracking small juveniles at critical life stages where recruitment bottlenecks often manifest.
2. Stable isotope analysis (SIA) in consecutive laminae in eye lenses, a protein-rich depositional tissue, has emerged as a promising tool in fishes to develop long-term interpretive records of dietary histories using a single archival tissue. Currently, studies using fish eye lenses to study SIA in diets have primarily been conducted in marine environments using $\delta^{13}C$ and $\delta^{15}N$ to identify resource partitioning, ontogenetic shifts and lifelong trophic histories. To date, no studies have examined freshwater taxa nor used $\delta^{34}S$ isotopes.
3. We placed juvenile (Chinook Salmon) *Oncorhynchus tshawytscha* in experimental enclosures in three different freshwater habitats (hatchery, river and seasonal floodplain), each with isotopically distinct and well-characterized food webs. This experimental approach allowed us to directly measure diets and quantify tissue turnover rates in eye lenses as well as the isotopic fractionation among fish tissues (fin and muscle tissue) in distinct habitat types using stable isotopes $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$.
4. Bulk eye-lens stable isotope measurements were analysed for juvenile salmon lenses and were found to be consistent with the isotopic values of rearing habitats. Slight additional isotopic fractionation was only found in $\delta^{13}C$. We then successfully applied the method to a larger, reproductively mature adult salmon captured in freshwater and inferred juvenile habitat use.
5. SIA in eye lenses using three dietary isotopes ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$) has significant potential for answering critical questions about migration, diet, foraging ecology and life history of migratory aquatic animals on Earth. Such information would have immediate application towards conservation management of diverse species and habitats at multiple scales.

KEYWORDS

carbon, floodplain, habitat use, nitrogen, ontogeny, stable isotopes, sulphur

1 | INTRODUCTION

Migratory aquatic animals face unparalleled challenges (Runge et al., 2014). For the vast majority of species, data on ecological and behavioural patterns and impacts from humans are lacking (Phillis et al., 2018; Vitule et al., 2017). To complete complex life cycles, mobile animals often require specific habitats for relatively brief but essential periods (Block et al., 2011; Grol et al., 2014). Ineffective conservation strategies often stem from missing information on species–habitat relationships during critical periods (Sass et al., 2017). New methods are needed to uncover these dynamics for species conservation.

Stable isotope analysis (SIA) is increasingly routine for studying animal migrations, provided predictable turnover rates in tissues and spatial differences in isotopic ratios (Heady & Moore, 2013; Hobson & Wassenaar, 2018; Philp, 2007; West et al., 2006). Yet, applying SIA to biominerals, such as otoliths that have the potential to reconstruct diet chronologies in a single structure, is uncommon (Grønkjær et al., 2013; McMahon et al., 2011; Weber et al., 2002). This is due to otoliths being composed primarily of calcium carbonate and inorganic forms of carbon, with minimal protein (<1%–10%), which limit these structures as dietary isotopic time-series recorders (see exceptions, M. Bell-Tilcock, C. Jeffres, A. Rypel, M. Wilmes, R. Armstrong, P. Holden, P. Moyle, N. Fangue, J. Katz, T. Sommer, J. Conrad, & R. Johnson, unpubl. data; Johnson et al., 2012; Lueders-Dumont et al., 2018; Weber et al., 2002).

SIA in protein-rich eye lenses of fish tracks dietary isotopic values over a lifespan (Curtis et al., 2020; Kurth et al., 2019; Quaeck-Davies et al., 2018; Simpson et al., 2019; Tzadik et al., 2017; Vecchio et al., 2021; Vecchio & Peebles, 2020; Wallace et al., 2014). Fish eye lenses are small, onion-like spheres composed of layers (laminae), forming continuously over life, and are no longer undergoing protein synthesis once fully formed (Granneman, 2018; Greiling & Clark, 2012; Nicol, 1973; Tzadik et al., 2017; Vecchio, 2020; Wallace et al., 2014; Wride, 2011). Currently, little is known on mechanisms influencing frequency of individual lens laminae formation; however, previous work has described dynamics of isotopic turnover of lens tissue (Granneman, 2018). A strong relationship exists within a species between body size and lens diameter, with laminae forming during periods of somatic growth (Quaeck-Davies et al., 2018; Granneman, 2018; Kurth et al., 2019; Vecchio & Peebles, 2020; Vecchio et al., 2021). Variation in $\delta^{13}C$ and $\delta^{15}N$ between left and right lens tissue is negligible, allowing laminae from each eye to be combined to provide sufficient sample for isotope analyses in smaller organisms (Wallace et al., 2014; M. Young, V. Larwood, J. Clause, M. Bell-Tilcock, G. Whitman, R. Johnson, & F. Feyrer, unpubl. data). Previous work has focused on resource partitioning, ontogenetic shifts and lifelong trophic histories of fishes and cephalopods in marine systems (Liu et al., 2020; Meath et al., 2019; Quaeck-Davies et al., 2018; Simpson et al., 2019; Tzadik et al., 2017; Vecchio & Peebles, 2020; Wallace et al., 2014; Xu et al., 2019). Importantly, no work has occurred on this technique for freshwater nor anadromous species despite its potential to chronicle movement and life history of diverse fishes, many of which are declining (Moyle & Leidy, 1992; West et al., 2006).

Dietary stable isotopes are divergent among freshwater, wetland and marine systems making them ideal to track landscape-scale and finer-scale habitat use across these gradients. The use of $\delta^{13}C$ is often linked to energy flows in a system where ocean $\delta^{13}C$ values are higher compared to many terrestrial and freshwater inputs (Chaloner et al., 2002). $\delta^{15}N$ is used to quantify trophic position in a food web because there is 3‰–4‰ enrichment with each consumer (Fry, 2006). Therefore, salmon feeding on freshwater aquatic insects has different $\delta^{15}N$ than salmon in hatcheries that feed higher trophically on marine sources of protein in their feed (Hurd et al., 2008). Within freshwater and estuarine systems, habitats such as tidal wetlands and fluvial floodplains that have large pools of organic matter and long water residence times have exceptionally low $\delta^{34}S$ values (Limburg et al., 2015; Schlesinger & Bernhardt, 2013). Isotopic gradients in $\delta^{13}C$, $\delta^{15}N$, $\delta^{18}O$, $\delta^{34}S$ and $^{87}Sr/^{86}Sr$ are well characterized across the landscape of habitats used by juvenile Chinook Salmon *(Oncorhynchus tshawytscha)* in California's Central Valley (USA) making it a model system for advancing the use of eye-lens isotopes in fish ecology (Barnett-Johnson et al., 2008; Downing et al., 2016; Eckard et al., 2007; Johnson et al., 2012; Tomkovic et al., 2020).

We conducted, for the first time, field-based diet experiments where juvenile salmon were reared for known durations in three distinct food webs (river, floodplain and hatchery) that characterize the three dominant freshwater rearing habitats for salmon in California's Central Valley (Moyle & Leidy, 1992). Our goals were to (a) document the distinctiveness of the isotopic values in each food web studied; (b) quantify $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values as they are integrated from diet into fish lenses and (c) examine whether this method holds promise for generating long-term interpretive records in adult animals. Advancement of this method for reconstructing smaller-scale movements and diet reconstructions across multiple aquatic systems have immediate implications for the study and conservation of freshwater and migratory species.

2 | MATERIALS AND METHODS

2.1 | Study system

The Mediterranean climate of the Central Valley supports four evolutionarily distinct runs of Chinook Salmon that occupy the watershed year round, all of which are in various stages of decline (Moyle et al., 2011; Yoshiyama et al., 1998). During wet years, remnant floodplain habitat exists for juvenile salmonids, but mostly within managed flood basins (i.e. Sutter and Yolo Bypasses, Figure 1). When floodplains are not available, migrating juvenile Chinook Salmon are relegated to the main river channel. The Sacramento River is California's largest river. Its lower 245 km are channelized and leveed, effectively reducing the amount of natural floodplain available for Chinook Salmon (Figure 1; Sommer et al., 2001). Yet, the relative importance of floodplains to the survival and recruitment dynamics of Chinook Salmon remains an outstanding question in the conservation and management of the species.

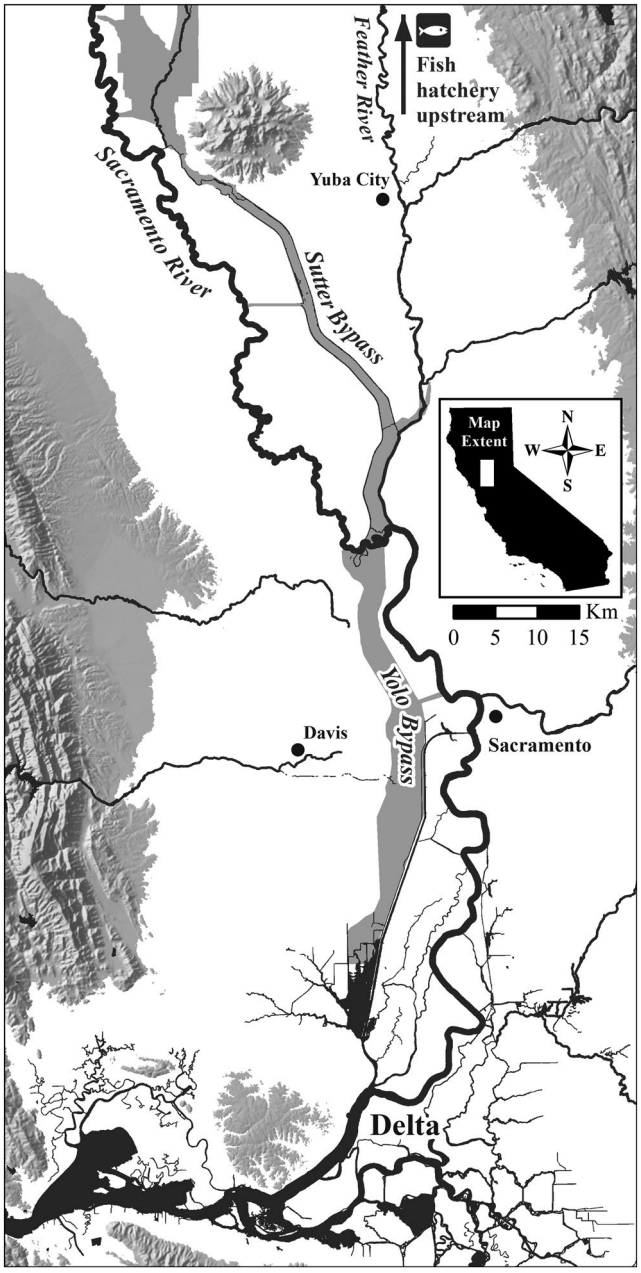

FIGURE 1 Map of study system, including the Feather River Hatchery, lotic Sacramento River, and the Yolo Bypass

2.2 | Field experiment and wild fish

We build on the landscape-scale experimental floodplain ecology research outlined in Jeffres et al. (2020) to include a dietary reconstruction component using isotopes. Briefly, hatchery-origin juvenile Chinook Salmon were released within experimental managed floodplain fields in 2016 and captured weekly with some retained to characterize the isotopic baseline for the hatchery (Figure 1; Table 1). As part of the same experiment, fish were placed in enclosures in the Sacramento River to characterize growth and food web isotope signatures. To assess the relationship among tissues in wild-caught salmon compared to enclosed river fish, juvenile salmon were captured concurrently in the Sacramento River channel by the Delta Juvenile Fish Monitoring Program (DJFMP) using a 15m beach seine, midwater trawl and Kodiak trawl (Table 1; Mitchell et al., 2019).

TABLE 1 List of tissue samples and lens tissues

Treatments	*N*	Tissue Type	Isotopes analysed
Juvenile Chinook Salmon reared in hatchery (*N* = 3), enclosures in the Sacramento River (*N* = 1), wild in the Sacramento River (*N* = 3), on the Yolo Bypass floodplain (*N* = 4)	11	Whole lens minus the core	$\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$
Juvenile Chinook Salmon (9–39 days on the Yolo Bypass floodplain)*	45	Stomach contents	$\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$
Juvenile Chinook Salmon (9–39 days on the Yolo Bypass floodplain)*	30	Fin tissue	$\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$
Juvenile Chinook Salmon (0–39 days on the Yolo Bypass floodplain)*	60	Muscle tissue	$\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$
Juvenile Chinook Salmon (*N* = 1) from the Feather River Hatchery were reared on the Yolo Bypass floodplain for 39 days	1	Individual Laminae	$\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$
Adult Chinook Salmon (Yolo Bypass)	1	Individual laminae	$\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$

*Data from these fish can be found in Tilcock (2019) and M. Bell-Tilcock, C. Jeffres, A. Rypel, M. Wilmes, R. Armstrong, P. Holden, P. Moyle, N. Fangue, J. Katz, T. Sommer, J. Conrad and R. Johnson (unpubl. data).

2.3 | Lens Technique

Lenses were removed by creating an incision near the top of the eye and extracting each lens with a pair of forceps. Once the lens capsule was removed, lenses were delaminated using a modification of techniques described in Wallace et al. (2014) (Supporting information). Laminae were dried in pre-weighed 8 mm × 5 mm tin capsules (Elemental Microanalysis pressed tin capsules) and submitted to the UC Davis Stable Isotope Facility for combined $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ analysis.

2.4 | Landscape-scale variation in isotopes across habitats

Laminae from both eyes of individual fish were combined for bulk analyses to meet minimum dry weight requirements for combined $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ analysis (2 mg). The lens core was omitted to eliminate maternal marine bias, due to salmon spending approximately a month feeding from a yolk sac composed of maternal marine protein during development (Weber et al., 2002). The amount

of material from individuals in the Sacramento River enclosures was not sufficient to achieve the minimum dry weight. Therefore, lenses for these three individuals were combined and homogenized to produce a single value for this habitat. We tested reliability of lens isotopic dietary values to classify individuals into their correct rearing habitat using a linear discriminant analysis (LDA) utilizing jackknifed cross validation in the MASS package in R version 4.0.2 (Venables et al., 2002). Lastly, individual laminae from a single juvenile salmon from the floodplain were analysed for $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ to test the feasibility of reconstructing diets over smaller temporal and spatial scales of habitat use.

2.5 | $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ integration into fish tissues

Weekly dietary isotopic values in stomach contents, fin and muscle tissue were plotted from baseline hatchery values to 39 days on the floodplain. We then fit a LOESS curve with 95% CI (denoted in grey) to these data (M. Bell-Tilcock, C. Jeffres, A. Rypel, M. Wilmes, R. Armstrong, P. Holden, P. Moyle, N. Fangue, J. Katz, T. Sommer, J. Conrad, & R. Johnson, unpubl. data; Tilcock, 2019; Table 1). A formal statistical test was not conducted comparing these curves because we assume these relationships are inherently nonlinear, but nonetheless aim to describe general isotopic fractionation patterns as part of this study. Overall, C:N ratios were low within the muscle tissues (~3), suggesting lipid content is low enough in the muscle to not warrant correcting for fractionation (Post et al., 2007).

2.6 | Adult Salmon lifetime diet reconstruction

Fisheries managers in California clip the adipose fin of approximately 25%–30% of hatchery salmon (Kormos et al., 2012). In 2014, the carcass of one stray adult Chinook Salmon with intact adipose fin was recovered near our Yolo Bypass floodplain study site (Figure 1). The fish was transported to UC Davis where it was stored in a freezer until further processing. Using previously described methodology, individual laminae were separated and analysed for isotopic variations through time. Patterns in laminae isotopic variation were compared to known patterns in isotopic gradients across habitats.

3 | RESULTS

3.1 | Landscape-scale variation in isotopes across habitats

Eye-lens SIA differed in $\delta^{13}C$ values from salmon rearing across all three rearing habitats (Figure 2a; Table S1). Hatchery fish had the most enriched $\delta^{13}C$ values, with river-caught fish (−19.27‰ to −18.91‰) and enclosed river fish (−18.89‰) displaying more intermediate values. Fish reared on the floodplain for 39 days had the lowest values (−32.39‰ to −30.44‰), with 22-day floodplain reared showing intermediate values between hatchery-origin and 39-day floodplain samples (−26.62‰ to −26.44‰).

Similar differences existed in $\delta^{15}N$ values across all habitats (Figure 2b; Table S1). The most enriched values were found at the hatchery (14.50‰–15.58‰), with enclosed river fish (14.23‰) having $\delta^{15}N$ values similar to the hatchery. River-caught fish had intermediate values between the hatchery and floodplain (12.15‰–13.39‰). Unlike $\delta^{13}C$ however, $\delta^{15}N$ values for floodplain fish reared for 22 days (11.79‰–11.97‰) did not show an intermediate value and had a value similar to those reared for 39 days (11.20‰).

We found the largest range in isotopic values between habitats using $\delta^{34}S$ (Figure 2c; Table S1). The hatchery-origin fish had the most enriched values (15.35‰–17.62‰), with enclosed river fish (13.48‰) or captured in the river (14.09‰–14.41‰) having more depleted values compared to the hatchery. Similar to $\delta^{13}C$,

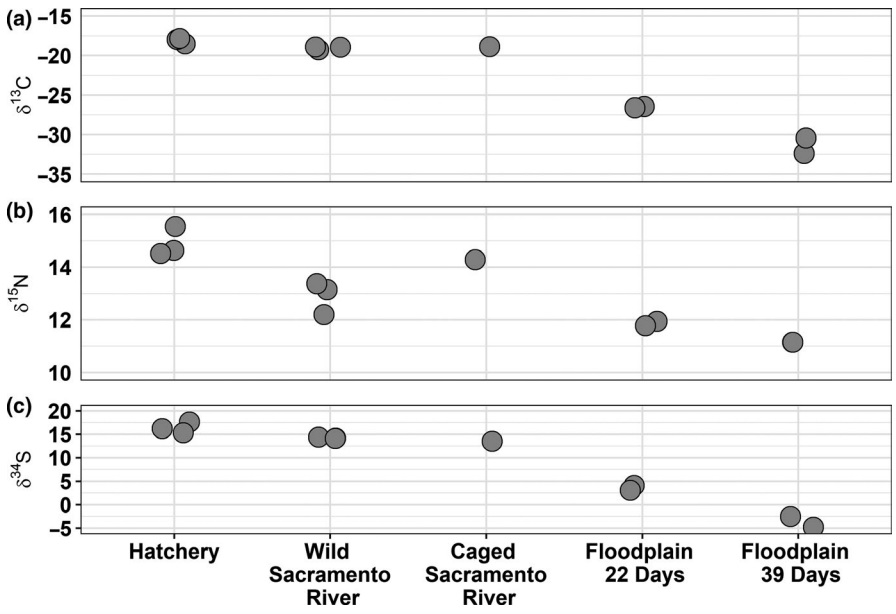

FIGURE 2 $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$ results from combined laminae (layer 1–4) by site ($N = 11$). Isotopic data from combined and homogenized laminae, excluding the core, highlighting differences in (a) $\delta^{13}C$, (b) $\delta^{15}N$ and (c) $\delta^{34}S$ values across habitat types

fish reared on the floodplain for 22 days had an intermediate value (3.12‰–4.09‰) from the hatchery compared to those reared on the floodplain for 39 days, which were the most depleted in $\delta^{34}S$ compared to other habitats (−2.56‰ to −4.78‰).

Classification accuracy of individual juvenile salmon to their known-rearing habitats using SIA in eye lenses and LDA sums were high overall, ranging from 72% to 91% (Table S3). When $\delta^{13}C$ and $\delta^{34}S$ were combined in the classification model, 91% of individuals were correctly classified to their rearing habitat (Table S3). The lowest classification accuracies occurred when only one isotope was used (72%–82%). Interestingly, the use of all three isotopes together produced a lower classification accuracy (82%) than any two isotopes together (all with 91% accuracy) likely due to $\delta^{15}N$ values being the most similar across habitats compared to $\delta^{13}C$ or $\delta^{34}S$.

Fish placed in experimental enclosures already had formed three laminae while in the hatchery, but by the end of the study had gained an additional lamina representing growth in their river or floodplain habitats (Figure 3). The $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values in the last laminae (#4) of the floodplain fish that reared for 39 days were in equilibrium with the bulk lens values for the same group (Figure 4). The earlier laminae (including the core) all had elevated $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ similar to ocean values likely due to the influence of marine protein from maternal sources and hatchery feed prior to arrival to the floodplain.

3.2 | $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values integrated into multiple fish tissues

SIA in all juvenile salmon tissues (Table 1; Tables S1 and S2) measured over the duration of the floodplain experiment declined from marine hatchery values to low floodplain values. Fractionation of 5.04‰ was found in $\delta^{13}C$ between mean diet and mean bulk lens and an additional fractionation of 3.47‰ from mean muscle to mean bulk lens (Figure 5a). We found an expected fractionation of 4.17‰ in $\delta^{15}N$ values between eye-lens values and diet but no additional fractionation occurred between bulk lens and other tissues (Figure 5b; Table S2). At the start of the experiment, $\delta^{34}S$ was 3.02‰ higher than muscle values. Yet by the termination of the study, bulk lens $\delta^{34}S$ and all other tissues converged on $\delta^{34}S$ diet values (Figure 5c; Table S2).

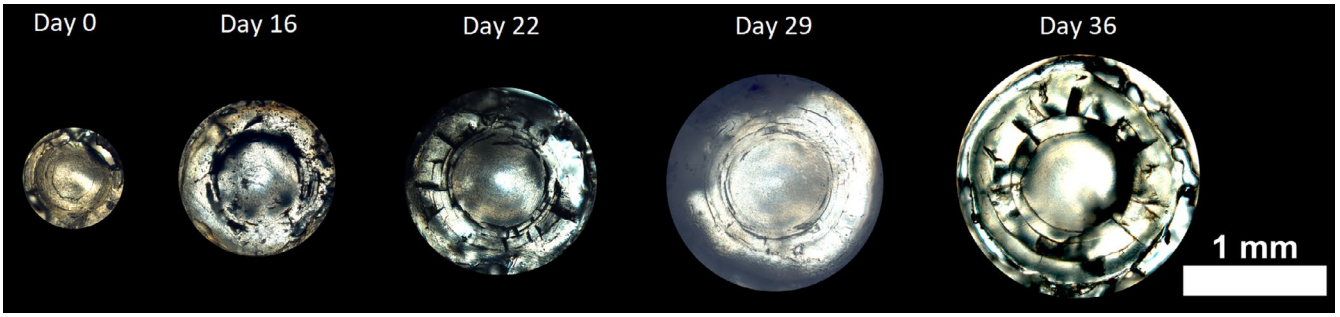

FIGURE 3 Cross section of juvenile Chinook salmon weekly lens growth on the Yolo Bypass. Time 0 represents fish from the hatchery arriving to the floodplain enclosure experiment detailed in Jeffres et al. (2020), then 16, 22, 29 and 36 days on the floodplain

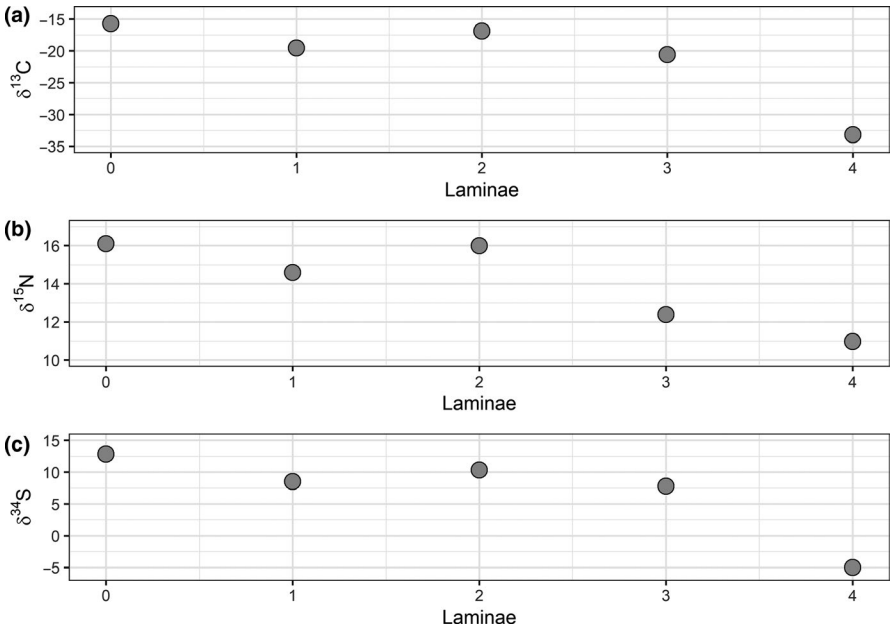

FIGURE 4 Isotopic values for (a) $\delta^{13}C$, (b) $\delta^{15}N$ and (c) $\delta^{34}S$ values of individual laminae from a juvenile Chinook Salmon that had reared for 39 days on the floodplain

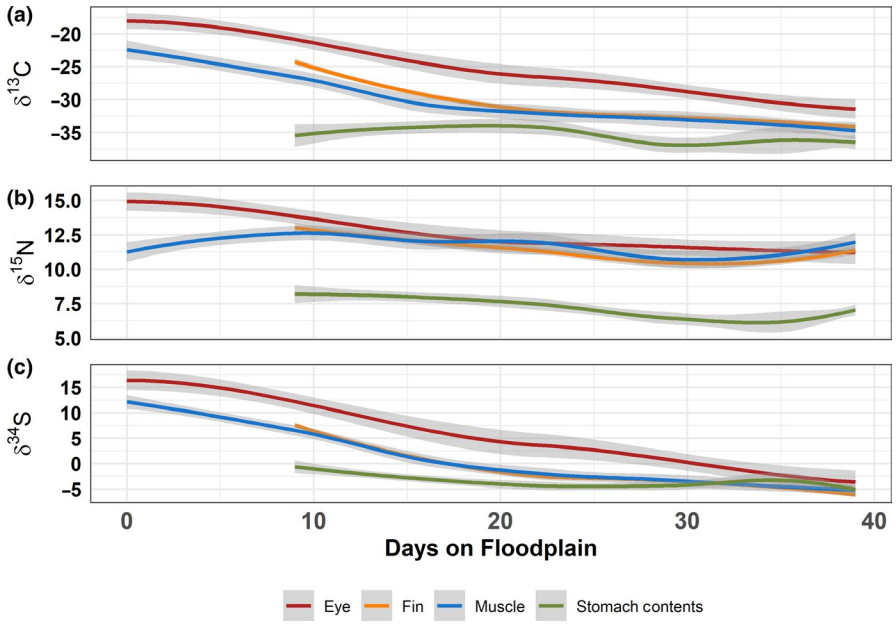

FIGURE 5 (a) Carbon ($\delta^{13}C$), (b) Nitrogen ($\delta^{15}N$) and (c) $\delta^{34}S$ values in stomach contents, fin tissue, muscle tissue, and eye lens from fish reared on the floodplain ($N = 7$). Plot adapted from Tilcock (2019) shows average $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ (and 95% confidence interval, shaded regions) in combined laminae, muscle tissue, fin, and stomach contents from fish reared on the floodplain for 39 days

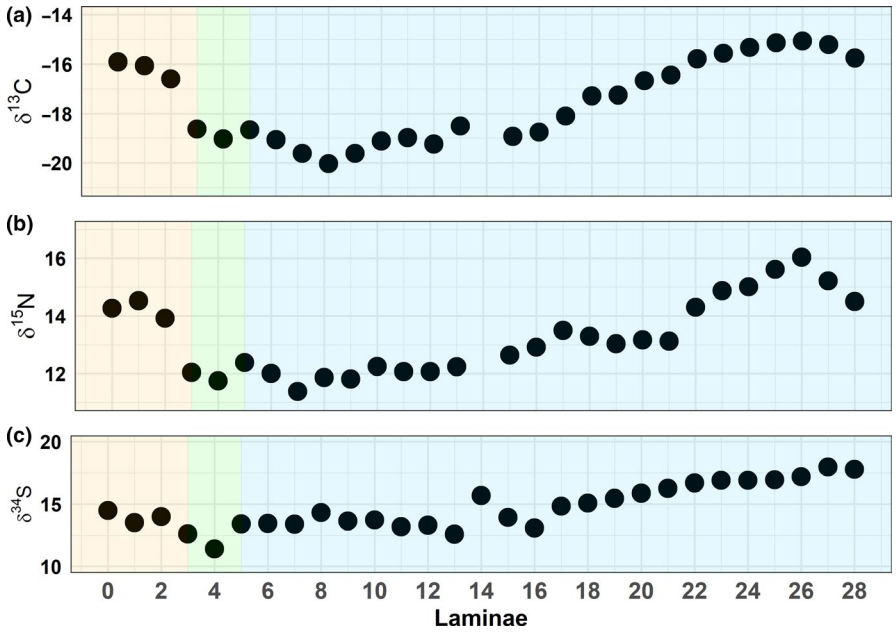

FIGURE 6 (a) $\delta^{13}C$, (b) $\delta^{15}N$ and (c) $\delta^{34}S$ values used to reconstruct habitat use in an adult Chinook Salmon. This fish originated from a hatchery (orange), was trucked to the estuary (green), and subsequently migrated to the ocean (blue)

3.3 | Adult Salmon lifetime diet reconstruction

We provide SIA for individual lamina of an adult salmon as a proof-of-concept on the relevance and application of this method to reconstruct fine-scale diet shifts across aquatic gradients that could be scaled up to population-level assessments. Generally, trends in isotopic values were consistent for all three isotopes. Beginning at the lens core, early laminae had $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values similar to ocean values, consistent with inherited maternal marine protein (Figure 6a–c, orange) and similar to the values seen in the corresponding laminae in juveniles. The laminae became lower through time, presumably as feeding on aquatic insects in riverine environments occurred (Figure 6a–c, green). Lamina eight was the lowest relative to other laminae. All isotope values steadily increased as the fish entered marine water and foraged on trophically higher prey. The final laminae values were similar to the SIA values of the first few laminae in the juveniles (Figure 6a–c, blue).

4 | DISCUSSION

Understanding how aquatic animals with complex behaviours and life cycles utilize diverse habitats is fundamental to their conservation (Hobson, 2008; Rubenstein & Hobson, 2004; Runge et al., 2014). The ability to track ontogenetic diet shifts in a single tissue provides key information on aquatic food webs, individual foraging ecology and contributions of habitats to aquatic

ecosystem productivity (Curtis et al., 2020; Kurth et al., 2019; Liu et al., 2020; Meath et al., 2019; Quaeck-Davies et al., 2018; Simpson et al., 2019; Vecchio & Peebles, 2020; Wallace et al., 2014; Xu et al., 2019).

The fractionation patterns found between the bulk lens analysis when compared to other tissues could be due to combining the laminae instead of analysing individual lamina. Even still, the $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values in combined laminae reliably identified which individuals reared on the floodplain, river or hatchery. Although our sample sizes were relatively small, the isotopic signals were consistent with previous work showing significant differences in all isotopes across all three habitat types. These results therefore represent another study supporting the usefulness of eye-lens SIA using bulk lens analysis (Meath et al., 2019; Vecchio, 2020), as well as demonstrate new applications for reconstructing trophic life histories of migratory fish.

Future research should further explore frequency of lens layer formation across a variety of fish species and other aquatic animals. Fish reared in floodplain habitats grew rapidly and appeared to add an additional lamina during the 39-day duration of the study compared to fish reared in river or hatchery (Figure 2). While frequency of lens layer formation remains unknown, lenses in floodplain-reared fish were in isotopic equilibrium with their muscle tissue by the conclusion of the study (39 days). The assimilation rate in these lenses was similar to Granneman et al. (2018), yet muscle assimilation rate was faster than previously seen in laboratory studies (Heady & Moore, 2013). This is likely due to rapid growth rates occurring on the floodplain for these fish (Jeffres et al., 2020). Nevertheless, better methods to understand frequency and mechanisms of layer formulation would be valuable to strengthen our understanding of the temporal resolution of eye lenses for diet reconstructions in salmon and other species.

This method opens avenues in aquatic conservation ecology for more than Pacific salmonids in California. Migratory species as juvenile fish rear in a variety of habitats throughout their life history (Grol et al., 2014; Kimirei et al., 2013; Rypel et al., 2012; Subalusky et al., 2009; Werner & Hall, 1988). Higher-resolution data with respect to habitat use are needed to advance conservation and management of declining aquatic taxa. In our study, SIA in eye lenses provides a potentially valuable tool for quantifying the role of floodplains, notably their contribution to recruitment and production of adult populations and the fishery. Additionally, the isotopic patterns seen in the adult salmon reconstruction were similar to what has previously been documented in the ocean (Hertz et al., 2015; Kaeriyama et al., 2004; Satterfield IV & Finney, 2002; Welch & Parsons, 1993). Lens SIA provides an opportunity to better understand changes in marine food webs as ocean conditions shift with climate change. Documenting ocean and freshwater patterns may lead to greater protection and restoration of habitats, which could, in turn, aid in the recovery of imperiled salmon populations. The use of lens SIA on a broad scale could yield substantial increases in the quantity and quality of life-history information for diverse fish species in addition to critical habitat needs of taxa (Sass et al., 2017).

ACKNOWLEDGEMENTS

Amber Manfree, Mollie Ogaz, Dana Myers, Kelly Neal, Anna Sturrock, Veronica Corbett, Eric Holmes, Rosa Cox, Emma Cox, Lily Tomkovick, UC Davis Stable Isotope Facility, Delta Juvenile Fish Monitoring Program, and California Department of Fish and Wildlife provided invaluable project assistance and sample collection. Authors declare no conflicts of interests.

AUTHORS' CONTRIBUTIONS

C.A.J., T.R.S., J.V.E.K. and M.B.-T. conceived and designed the field experiments; M.B.-T., C.A.J., G.W. and R.C.J. conceived the ideas and designed laboratory methodology; M.B.T. and G.W. collected the laboratory data; M.B.-T., C.A.J., A.L.R. and R.C.J. analysed the data; M.B.-T., C.A.J., A.L.R., T.R.S., J.V.E.K. and R.C.J. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Peer Review

The peer review history for this article is available at https://publons.com/publon/10.1111/2041-210X.13543.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository https://doi.org/10.25338/B8WW5D (Bell-Tilcock et al., 2021).

ORCID

Miranda Bell-Tilcock https://orcid.org/0000-0002-2714-2100
Carson A. Jeffres https://orcid.org/0000-0001-6532-6851
Andrew L. Rypel https://orcid.org/0000-0002-9812-8306
Ted R. Sommer https://orcid.org/0000-0001-6395-9831
Jacob V. E. Katz https://orcid.org/0000-0001-7842-4215
Rachel C. Johnson https://orcid.org/0000-0002-0278-7826

REFERENCES

Barnett-Johnson, R., Pearson, T. E., Ramos, F. C., Grimes, C. B., & Bruce MacFarlane, R. (2008). Tracking natal origins of salmon using isotopes, otoliths, and landscape geology. *Limnology and Oceanography*, *53*(4), 1633–1642. https://doi.org/10.4319/lo.2008.53.4.1633

Bell-Tilcock, M., Jeffres, C. A., Rypel, A. L., Sommer, T. R., Katz, J. V. E., Whitman, G., & Johnson, R. C. (2021). Data from: Advancing diet reconstuction in fish eye lenses. *Dryad Digital Repository*, https://doi.org/10.25338/B8WW5D

Block, B. A., Jonsen, I. D., Jorgensen, S. J., Winship, A. J., Shaffer, S. A., Bograd, S. J., Hazen, E. L., Foley, D. G., Breed, G. A., Harrison, A. L., Ganong, J. E., Swithenbank, A., Castleton, M., Dewar, H., Mate, B. R., Shillinger, G. L., Schaefer, K. M., Benson, S. R., Weise, M. J., … Costa, D. P. (2011). Tracking apex marine predator movements in a dynamic ocean. *Nature*, *475*(7354), 86–90. https://doi.org/10.1038/nature10082

Chaloner, D. T., Martin, K. M., Wipfli, M. S., Ostrom, P. H., & Lamberti, G. A. (2002). Marine carbon and nitrogen in southeastern Alaska stream food webs: Evidence from artificial and natural streams. *Canadian Journal of Fisheries and Aquatic Sciences*, *59*(8), 1257–1265. https://doi.org/10.1139/f02-084

Curtis, J. S., Albins, M. A., Peebles, E. B., & Stallings, C. D. (2020). Stable isotope analysis of eye lenses from invasive lionfish yields record of resource use. *Marine Ecology Progress Series*, *637*, 181–194. https://doi.org/10.3354/meps13247

Downing, B. D., Bergamaschi, B. A., Kendall, C., Kraus, T. E. C., Dennis, K. J., Carter, J. A., & Von Dessonneck, T. S. (2016). Using continuous underway isotope measurements to map water residence time in hydrodynamically complex tidal environments. *Environmental Science & Technology*, *50*(24), 13387–13396. https://doi.org/10.1021/acs.est.6b05745

Eckard, R. S., Hernes, P. J., Bergamaschi, B. A., Stepanauskas, R., & Kendall, C. (2007). Landscape scale controls on the vascular plant component of dissolved organic carbon across a freshwater delta. *Geochimica Et Cosmochimica Acta*, *71*(24), 5968–5984. https://doi.org/10.1016/j.gca.2007.09.027

Fry, B. (2006). *Stable isotope ecology*. Springer. https://doi.org/10.1007/0-387-33745-8

Granneman, J. E. (2018). Evaluation of trace-metal and isotopic records as techniques for tracking lifetime movement patterns in fishes. Graduate Theses and Dissertations. https://scholarcommons.usf.edu/etd/7675

Greiling, T. M. S., & Clark, J. I. (2012). New insights into the mechanism of lens development using zebra fish. *International Review of Cell and Molecular Biology*, *296*, 1–61. https://doi.org/10.1016/B978-0-12-394307-1.00001-1

Grol, M. G. G., Rypel, A. L., & Nagelkerken, I. (2014). Growth potential and predation risk drive ontogenetic shifts among nursery habitats in a coral reef fish. *Marine Ecology Progress Series*, *502*, 229–244. https://doi.org/10.3354/meps10682

Grønkjær, P., Pedersen, J. B., Ankjærø, T. T., Kjeldsen, H., Heinemeier, J., Steingrund, P., Nielsen, J. M., & Christensen, J. T. (2013). Stable N and C isotopes in the organic matrix of fish otoliths: Validation of a new approach for studying spatial and temporal changes in the trophic structure of aquatic ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences*, *70*(2), 143–146. https://doi.org/10.1139/cjfas-2012-0386

Heady, W. N., & Moore, J. W. (2013). Tissue turnover and stable isotope clocks to quantify resource shifts in anadromous rainbow trout. *Oecologia*, *172*(1), 21–34. https://doi.org/10.1007/s00442-012-2483-9

Hertz, E., Trudel, M., Brodeur, R. D., Daly, E. A., Eisner, L., Farley, E. V., Harding, J. A., MacFarlane, R. B., Mazumder, S., Moss, J. H., Murphy, J. M., & Mazumder, A. (2015). Continental-scale variability in the feeding ecology of juvenile Chinook salmon along the coastal Northeast Pacific Ocean. *Marine Ecology Progress Series*, *537*, 247–263. https://doi.org/10.3354/meps11440

Hobson, K. A. (2008). Applying isotopic methods to tracking animal movements. *Terrestrial Ecology*, *2*, 45–78. https://doi.org/10.1016/S1936-7961(07)00003-6

Hobson, K. A., & Wassenaar, L. I. (2018). *Tracking animal migration with stable isotopes*. Academic Press. https://doi.org/10.1016/C2017-0-01125-4

Hurd, T. M., Jesic, S., Jerin, J. L., Fuller, N. W., & Miller, D. (2008). Stable isotope tracing of trout hatchery carbon to sediments and foodwebs of limestone spring creeks. *Science of the Total Environment*, *405*(1–3), 161–172. https://doi.org/10.1016/j.scitotenv.2008.06.036

Jeffres, C. A., Holmes, E. J., Sommer, T. R., & Katz, J. V. E. (2020). Detrital food web contributes to aquatic ecosystem productivity and rapid salmon growth in a managed floodplain. *PLoS One*, https://doi.org/10.1371/journal.pone.0216019

Johnson, R. C., Weber, P. K., Wikert, J. D., Workman, M. L., Macfarlane, R. B., Grove, M. J., & Schmitt, A. K. (2012). Managed metapopulations: Do salmon hatchery 'sources' lead to in-river 'sinks' in conservation? *PLoS ONE*, *7*(2), e28880. https://doi.org/10.1371/journal.pone.0028880

Kaeriyama, M., Nakamura, M., Edpalina, R., Bower, J. R., Yamaguchi, H., Walker, R. V., & Myers, K. W. (2004). Change in feeding ecology and trophic dynamics of Pacific salmon (*Oncorhynchus* spp.) in the central Gulf of Alaska in relation to climate events. *Fisheries Oceanography*, *13*(3), 197–207. https://doi.org/10.1111/j.1365-2419.2004.00286.x

Kimirei, I. A., Nagelkerken, I., Trommelen, M., Blankers, P., van Hoytema, N., Hoeijmakers, D., Huijbers, C. M., Mgaya, Y. D., & Rypel, A. L. (2013). What drives ontogenetic niche shifts of fishes in coral reef ecosystems? *Ecosystems*, *16*(5), 783–796. https://doi.org/10.1007/s10021-013-9645-4

Kormos, B., Palmer-Zwahlen, M., & Low, A. (2012). *Recovery of coded-wire tags from Chinook Salmon in California's central valley escapement and ocean harvest in 2010*. Fisheries Branch Administrative Report 2013-02.

Kurth, B. N., Peebles, E. B., & Stallings, C. D. (2019). Atlantic Tarpon (*Megalops atlanticus*) exhibit upper estuarine habitat dependence followed by foraging system fidelity after ontogenetic habitat shifts. *Estuarine, Coastal and Shelf Science*, *225*, 106248. https://doi.org/10.1016/j.ecss.2019.106248

Limburg, K. E., Walther, B. D., Lu, Z., Jackman, G., Mohan, J., Walther, Y., Nissling, A., Weber, P. K., Schmitt, A. K., & Schmitt, A. K. (2015). In search of the dead zone: Use of otoliths for tracking fish exposure to hypoxia. *Journal of Marine Systems*, *141*, 167–178. https://doi.org/10.1016/j.jmarsys.2014.02.014

Liu, B. L., Xu, W., Chen, X. J., Huan, M. Y., & Liu, N. (2020). Ontogenetic shifts in trophic geography of jumbo squid, *Dosidicus gigas*, inferred from stable isotopes in eye lens. *Fisheries Research*, *226*, 105507. https://doi.org/10.1016/j.fishres.2020.105507

Lueders-Dumont, J. A., Wang, X. T., Jensen, O. P., Sigman, D. M., & Ward, B. B. (2018). Nitrogen isotopic analysis of carbonate-bound organic matter in modern and fossil fish otoliths. *Geochimica et Cosmochimica Acta*, *241*, 200–222. https://doi.org/10.1016/j.gca.2018.01.001

McMahon, K. W., Fogel, M. L., Johnson, B. J., Houghton, L. A., & Thorrold, S. R. (2011). A new method to reconstruct fish diet and movement patterns from $\delta^{13}C$ values in otolith amino acids. *Canadian Journal of Fisheries and Aquatic Sciences*, *68*, 1330–1340. https://doi.org/10.1139/f2011-070

Meath, B., Peebles, E. B., Seibel, B. A., & Judkins, H. (2019). Stable isotopes in the eye lenses of *Doryteuthis plei* (Blainville 1823): Exploring natal origins and migratory patterns in the eastern Gulf of Mexico. *Continental Shelf Research*, *174*, 76–84. https://doi.org/10.1016/j.csr.2018.12.013

Mitchell, L., Newman, K., & Baxter, R. (2019). Estimating the size selectivity of fishing trawls for a short-lived fish species. *San Francisco Estuary and Watershed Science*, *17*(1), 1–24. https://doi.org/10.15447/sfews.2019v17iss1art5; https://escholarship.org/uc/item/0hh7n9x2

Moyle, P. B., Katz, J. V. E., & Quiñones, R. M. (2011). Rapid decline of California's native inland fishes: A status assessment. *Biological Conservation*, *144*(10), 2414–2423. https://doi.org/10.1016/j.biocon.2011.06.002

Moyle, P. B., & Leidy, R. A. (1992). Loss of biodiversity in ecosystems: Evidence from fish faunas. In P. L. Fiedler, & S. K. Jain (Eds.), *Conservation biology: The theory and practice of nature conservation, preservation and management*. (127–169). Chapman and Hall.

Nicol, J. A. C. (1973). Studies on the eyes of gars (Lepisosteidae) with special reference to the tapetum lucidum. *Canadian Journal of Zoology*, *51*(5), 501–508. https://doi.org/10.1139/z73-075

Phillis, C. C., Sturrock, A. M., Johnson, R. C., & Weber, P. K. (2018). Endangered winter-run Chinook salmon rely on diverse rearing habitats in a highly altered landscape. *Biological Conservation*, *217*, 358–362. https://doi.org/10.1016/j.biocon.2017.10.023

Philp, R. P. (2007). The emergence of stable isotopes in environmental and forensic geochemistry studies: A review. *Environmental Chemistry Letters*, *5*(2), 57–66. https://doi.org/10.1007/s10311-006-0081-y

Post, D. M., Layman, C. A., Arrington, D. A., Takimoto, G., Quattrochi, J., & Montaña, C. G. (2007). Getting to the fat of the matter: Models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia*, *152*(1), 179–189. https://doi.org/10.1007/s00442-006-0630-x

Quaeck-Davies, K., Bendall, V. A., MacKenzie, K. M., Hetherington, S., Newton, J., & Trueman, C. N. (2018). Teleost and elasmobranch eye lenses as a target for life-history stable isotope analyses. *PeerJ*, *6*, e4883. https://doi.org/10.7717/peerj.4883

Rubenstein, D. R., & Hobson, K. A. (2004). From birds to butterflies: Animal movement patterns and stable isotopes. *Trends in Ecology & Evolution*, *19*(5), 256–263. https://doi.org/10.1016/j.tree.2004.03.017

Runge, C. A., Martin, T. G., Possingham, H. P., Willis, S. G., & Fuller, R. A. (2014). Conserving mobile species. *Frontiers in Ecology and the Environment*, *12*(7), 395–402. https://doi.org/10.1890/130237

Rypel, A. L., Pounds, K. M., & Findlay, R. H. (2012). Spatial and temporal trade-offs by bluegills in floodplain river ecosystems. *Ecosystems*, *15*(4), 555–563. https://doi.org/10.1007/s10021-012-9528-0

Sass, G. G., Rypel, A. L., & Stafford, J. D. (2017). Inland fisheries habitat management: Lessons learned from wildlife ecology and a proposal for change. *Fisheries*, *42*(4), 197–209. https://doi.org/10.1080/03632415.2017.1276344

Satterfield, F. R. IV, & Finney, B. P. (2002). Stable isotope analysis of Pacific salmon: Insight into trophic status and oceanographic conditions over the last 30 years. *Progress in Oceanography*, *53*(2–4), 231–246. https://doi.org/10.1016/S0079-6611(02)00032-0

Schlesinger, W. H., & Bernhardt, E. S. (2013). *Biogeochemistry. An analysis of global change*. Academic Press. https://doi.org/10.1016/C2010-0-66291-2

Simpson, S. J., Sims, D. W., & Trueman, C. N. (2019). Ontogenetic trends in resource partitioning and trophic geography of sympatric skates (Rajidae) inferred from stable isotope composition across eye lenses. *Marine Ecology Progress Series*, *624*, 103–116. https://doi.org/10.3354/meps13030

Sommer, T. R., Nobriga, M. L., Harrell, W. C., Batham, W., & Kimmerer, W. J. (2001). Floodplain rearing of juvenile chinook salmon: Evidence of enhanced growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*(2), 325–333. https://doi.org/10.1139/f00-245

Subalusky, A. L., Fitzgerald, L. A., & Smith, L. L. (2009). Ontogenetic niche shifts in the American Alligator establish functional connectivity between aquatic systems. *Biological Conservation*, *142*(7), 1507–1514. https://doi.org/10.1016/j.biocon.2009.02.019

Tilcock, M. N. (2019). Isotope tools to track floodplain rearing of juvenile chinook salmon (Order No. 13862230). Available from Dissertations & Theses at University of California; ProQuest Dissertations & Theses A&I. (2299216518). https://search.proquest.com/docview/2299216518?accountid=14505

Tomkovic, L. A., Gross, E. S., Nakamoto, B., Fogel, M. L., & Jeffres, C. (2020). Source water apportionment of a river network: Comparing field isotopes to hydrodynamically modeled tracers. *Water*, *12*(4), 1128–https://doi.org/10.3390/w12041128

Tzadik, O. E., Curtis, J. S., Granneman, J. E., Kurth, B. N., Pusack, T. J., Wallace, A. A., Hollander, D. J., Peebles, E. B., & Stallings, C. D. (2017). Chemical archives in fishes beyond otoliths: A review on the use of other body parts as chronological recorders of microchemical constituents for expanding interpretations of environmental, ecological, and life-history changes. *Limnology and Oceanography: Methods*, *15*(3), 238–263. https://doi.org/10.1002/lom3.10153

Vecchio, J. L. (2020). Isotope-based methods for evaluating fish trophic geographies. Graduate Theses and Dissertations. https://scholarcommons.usf.edu/etd/8306

Vecchio, J. L., Ostroff, J. L., & Peebles, E. B. (2021). Isotopic characterization of lifetime movement by two demersal fishes from the northeastern Gulf of Mexico. *Marine Ecology Progress Series*, *657*, 161–172. https://doi.org/10.3354/meps13525

Vecchio, J. L., & Peebles, E. B. (2020). Spawning origins and ontogenetic movements for demersal fishes: An approach using eye-lens stable isotopes. *Estuarine, Coastal and Shelf Science*, *246*, 107047. https://doi.org/10.1016/j.ecss.2020.107047

Venables, W. N., & Ripley, B. D. (2002). Ch 12. Classification. In J. Chambers, W. Eddy, W. Hardle, S. Sheather, & L. Tierney (Eds.), *Modern applied statistics with S4* (pp. 331–351). Springer.

Vitule, J. R. S., Agostinho, A. A., Azevedo-Santos, V. M., Daga, V. S., Darwall, W. R. T., Fitzgerald, D. B., Frehse, F. A., Hoeinghaus, D. J., Lima-Junior, D. P., Magalhães, A. L. B., Orsi, M. L., Padial, A. A., Pelicice, F. M., Petrere, M., Pompeu, P. S., & Winemiller, K. O. (2017). We need better understanding about functional diversity and vulnerability of tropical freshwater fishes. *Biodiversity and Conservation*, *26*(3), 757–762. https://doi.org/10.1007/s10531-016-1258-8

Wallace, A. A., Hollander, D. J., & Peebles, E. B. (2014). Stable isotopes in fish eye lenses as potential recorders of trophic and geographic history. *PLoS ONE*, *9*(10), e108935. https://doi.org/10.1371/journal.pone.0108935

Weber, P. K., Hutcheon, I. D., Mckeegan, K. D., & Ingram, B. L. (2002). Otolith sulfur isotope method to reconstruct salmon (*Oncorhynchus tshawytscha*) life history. *Canadian Journal of Fisheries and Aquatic Sciences*, *591*, 587–591. https://doi.org/10.1139/F02-038

Welch, D. W., & Parsons, T. R. (1993). $\delta^{13}C$–$\delta^{15}N$ values as indicators of trophic position and competitive overlap for Pacific salmon (*Oncorhynchus* spp.). *Fisheries Oceanography*, *2*(1), 11–23. https://doi.org/10.1111/j.1365-2419.1993.tb00008.x

Werner, E. E., & Hall, D. J. (1988). Ontogenetic habitat shifts in bluegill: The foraging rate-predation risk trade-off. *Ecology*, *69*(5), 1352–1366. https://doi.org/10.2307/1941633

West, J. B., Bowen, G. J., Cerling, T. E., & Ehleringer, J. R. (2006). Stable isotopes as one of nature's ecological recorders. *Trends in Ecology & Evolution*, *21*(7), 408–414. https://doi.org/10.1016/j.tree.2006.04.002

Wride, M. A. (2011). Lens fibre cell differentiation and organelle loss: Many paths lead to clarity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1568), 1219–1233. https://doi.org/10.1098/rstb.2010.0324

Xu, W., Chen, X., Liu, B., Chen, Y., Huan, M., Liu, N., & Lin, J. (2019). Inter-individual variation in trophic history of *Dosidicus gigas*, as indicated by stable isotopes in eye lenses. *Aquaculture and Fisheries*, *4*, 261–267. https://doi.org/10.1016/j.aaf.2019.05.001

Yoshiyama, R. M., Fisher, F. W., & Moyle, P. B. (1998). Historical abundance and decline of chinook salmon in the Central Valley Region of California. *North American Journal of Fisheries Management*, *18*(3), 487–521. https://doi.org/10.1577/1548-8675(1998)018<0487:haadoc>2.0.co;2

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Bell-Tilcock M, Jeffres CA, Rypel AL, et al. Advancing diet reconstruction in fish eye lenses. *Methods Ecol Evol*. 2021;12:449–457. https://doi.org/10.1111/2041-210X.13543