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EDITORIAL

Frontiers in otolith chemistry: insights, advances and applications

The rapid proliferation of publications employing chemical assays of fish hard parts, and otoliths in particular, has led to many novel insights into the migration patterns, life history strategies and mixed stock dynamics of fishes across the globe (Campana *et al.*, 2000; Elsdon *et al.*, 2008; Walther & Limburg, 2012). These insights include uncovering diverse migratory strategies within species and populations (Kerr *et al.*, 2009; Hogan *et al.*, 2014; Schoen *et al.*, 2016), quantifying rates of mixing among stocks across management boundaries (Rooker *et al.*, 2008; Walther & Thorrold, 2010) and estimating the relative importance of particular natal habitats for recruitment (Thorrold *et al.*, 2001; Schaffler *et al.*, 2015; Anstead *et al.*, 2016). Much of this work has been driven by advances in instrumentation that allow more precise and higher throughput analyses with greater spatial and temporal resolution for *in situ* assays of elemental and isotope constituents across otolith growth increments. Simultaneously, a smaller but growing number of carefully-designed experiments have provided essential validation for uptake and incorporation dynamics of elements into otoliths that underlie accurate interpretations of chemical composition patterns in wild-captured individuals (Sturrock *et al.*, 2014, 2015). This work has been increasingly focused on the possible confounding role of physiology in driving uptake dynamics, and the degree to which environmental and physiological factors influence specific elements. Together, these advances have prompted an increasing number of researchers to turn to otolith chemistry as a valuable tool to use alone or in combination with complementary approaches that may unravel critical questions in fish ecology. Much work, however, remains to be done to further develop this approach both to expand its utility and fully validate the environmental and biological mechanisms driving observed chemical patterns. To this end, the frontiers of otolith chemistry must be explored to ensure the field continues to mature during this period of explosive growth and widespread adoption.

This Special Issue grew out of an organized Symposium at the 2015 American Fisheries Society (AFS) annual meeting in Portland, Oregon, U.S.A. The symposium was jointly sponsored by the AFS Marine Fisheries Section (represented by B. Walther, Section President; C. Jones, Section President-Elect, and J. Schaffler, Section member) and the AFS Estuaries Section (represented by A. Archer, Section President, and K. Limburg, Section President-Elect). The scope of this symposium was broad and included advances in elemental and isotopic analysis of otoliths and analogous structures (*e.g.* scales, fin rays and vertebrae) in marine, diadromous and freshwater species, as well as studies that paired chemical analysis with complementary techniques (*e.g.* genetics, telemetry and soft tissue chemistry). In total, the symposium included 33 oral presentations and three associated posters from an international collection of researchers across the spectrum of career stages, and the resulting mix

of approaches, perspectives and conclusions provided a robust survey of the state of the field. Symposium participants were invited to submit their contributions to this Special Issue, and the nine manuscripts included here represent the diversity of studies presented at the symposium. Indeed, with the increased interest in and adoption of otolith chemistry techniques in the fish ecology and fisheries fields, organized publications and special issues collecting conference contributions have themselves proliferated in recent years (Begg *et al.*, 2005; Miller *et al.*, 2010; Morales-Nin & Geffen, 2015; Geffen *et al.*, 2016). The Special Issue here is the next chapter in this series of contributions, and below some of the notable insights and themes of the collected works are highlighted.

Elemental analyses of otoliths have been dominated by assays of a short list of elements, namely strontium (Sr) and barium (Ba). The focus on these elements stems from the idea that they are transported across membranes in concert with calcium (Ca) and are readily substituted for Ca in carbonate crystals. Further, it is generally accepted that the majority of Sr and Ba in otoliths derive from water and are therefore effective markers of environmental variation in these elements. Recent work has pointed out the potentially large influence of physiological regulation in affecting otolith chemistry patterns, particularly when ambient water concentrations of elements are relatively homogeneous or for elements such as magnesium (Mg) that do not appear to derive primarily from water. Thus the choice of element to investigate depends both on the question the worker wishes to resolve as well as the environmental and chemical gradients that may (or may not) exist across habitats. There is great interest in expanding the traditional suite of elements to others that may offer insight into other environmental gradients beyond salinity, including pH, hypoxia, pollution and upwelling. A primary limitation of such efforts remains the lack of experimental validations of uptake and incorporation dynamics of either new elements or previously-investigated elements in different physicochemical settings (such as experimentally manipulated pH, dissolved oxygen or water quality conditions).

Several of the contributions point out the necessity of validating basic assumptions about the chemical composition of otoliths as well as the selected analytical approach. Limburg & Elfman (2017) highlighted the potential for two-dimensional heterogeneity in composition of sectioned otoliths in elements such as strontium, barium, manganese and selenium but demonstrate the ability of microbeam methods for quantifying isotope ratios such as $\delta^{18}\text{O}$ values. A central assumption of most laser-based transect analyses of lifetime elemental profiles is that the choice of transect placement will not significantly affect the observed chemical patterns, but this work points out the need to revisit that assumption if certain elements are more readily incorporated into specific regions of an otolith. The processes mediating elemental uptake within the endoymph at the crystal interface are still poorly known. These processes deserve continued attention, particularly given the importance of the assumption of radially uniform uptake for interpreting chemical life history profiles. In addition, Pracheil *et al.* (2017) investigated the composition of acipenserid otoliths and found that the crystal form was heterogeneous with up to a third of the otoliths composed of calcite and the remainder vaterite, depending on the species. This heterogeneity of the CaCO_3 polymorph within and between otoliths is of particular concern given that polymorphs may incorporate trace elements at different rates and the calcium concentrations in polymorphs differ, necessitating polymorph-specific calibrations when expressing elemental ratios to calcium. Together, these contributions emphasize the need to carefully examine the underlying

assumptions when attempting to interpret otolith-derived migratory or environmental histories in wild-captured fishes, given the potential for violation of these assumptions to result in incorrect life history reconstructions.

Once otolith chemistry data are collected, appropriate statistical methods must be employed to accurately interpret elemental variation. One of the most common uses for otolith chemistry is assays of natal or nursery multi-elemental signatures to classify origins of wild-caught individuals to determine relative rates of contributions of spawning locations or rearing habitats. Critical to this approach is the appropriate selection of a classification method, with the current default being linear discriminant function analysis (LDFA). Otolith chemistry data, however, frequently violate several assumptions about distributions such as multivariate normality and equality of within-group covariance matrices that underlie LDFA. In an important assessment of this and alternative classification methods, Jones *et al.* (2017) assess classification performance of discriminant function analyses (linear and quadratic) as well as machine-algorithm methods when otolith data were non-normal and skewed with and without data transformations. When parametric assumptions were met, the traditional parametric classification methods performed best, indicating that when data can be transformed to meet assumptions, such as with the Box-Cox transformation, workers should proceed with parametric classifiers. This work highlights the need to carefully consider the statistical methods employed to classify unknown-origin individuals and not simply use approaches from previous studies as a default without inspecting data distributions at hand. At worst, such practices may lead to skewed conclusions about the relative contributions of certain sources to stock recruitment, with potentially serious consequences for ecological assessments of nursery function or management decisions.

Another important assumption underlying otolith chemistry analyses is that, for water-derived signatures, the spatial scale of ambient variation in signature values matches the scale of the ecological question under investigation. If a study is undertaken to resolve movements among tributaries, for instance, but all tributaries are chemically indistinguishable, an otolith chemistry approach will be useless for that study. Humston *et al.* (2017) address this issue by coupling model-derived estimates of spatial heterogeneity in water $^{87}\text{Sr}:^{86}\text{Sr}$ ratios with field-collected water samples to assess model performance in a mainstem and tributary system. Geospatial modelling of Sr 'isoscapes' have expanded in recent years given the ability to make first-order predictions of $^{87}\text{Sr}:^{86}\text{Sr}$ heterogeneity given that bedrock composition, age and weathering rates are known in many systems and are the dominant controls on dissolved Sr compositions in streams and rivers. Humston *et al.* (2017) employ a combined bedrock geology and chemical weathering model to predict that while tributaries could not be distinguished isotopically from one another, mainstem and tributary waters were sufficiently distinct to allow identification of migration into mainstem habitats. Water samples verified these predictions, and the study employed these markers to assess relative contributions of tributary spawning habitat and exchange among these two habitat types for a migratory centrarchid species. These modelling efforts should become increasingly important for constraining the scale at which otolith chemistry methods may be employed, particularly for $^{87}\text{Sr}:^{86}\text{Sr}$ models where the geological processes affecting isotope ratios are relatively well constrained. Future improvements to these models should focus on obtaining better estimates of weathering rates of

carbonates, quantifying potential inputs of groundwater endmembers and incorporating variable flow regimes that may alter contributions of upstream lithologies to downstream waters during periods of drought or flood.

In addition to otolith chemistry studies, a rapidly expanding area of interest is the use of alternative biological structures that may substitute as analogues for otoliths. These include scales, fin rays, vertebrae, scutes, eye lenses and beyond. The desire for such analogues is driven by (1) the need for structures that can be investigated in species that do not have otoliths, such as elasmobranchs, or those that can be sampled non-lethally for use with fishes that are imperiled, and (2) the search for complementary chemical information, given the possibility that these structures accumulate different suites of elements and isotopes or the same markers at different rates. In a comprehensive review of the use of elemental analyses in elasmobranch hard parts, McMillan *et al.* (2017) discuss the assumptions and limitations of these approaches similar to the assessment of Elsdon *et al.* (2008) for otoliths. McMillan *et al.* (2017) highlight the fact that elemental analyses in elasmobranchs is currently a young field, with few experimental validations of uptake and incorporation dynamics. Such studies will be essential for moving forward, particularly given that structures such as vertebrae are not aragonite but instead hydroxyapatite within a protein matrix with a relatively large organic fraction compared to otoliths. As such, investigators must be cautious not to apply otolith-derived uptake dynamics to these structures and are advised to continue experimental assessments to allow confidence in interpreting patterns from wild-caught specimens.

Three papers in this Special Issue validated the utility of otolith analogues and employed them to infer migratory movements of wild-captured fishes. First, Bock *et al.* (2017) quantified relationships of elemental and isotope ratios between water and dentary material in paddlefish *Polyodon spathula* (Walbaum 1792), and found strong support for the use of these markers in reconstructing water chemistry history with these structures. Dentary chemistry will be of great utility for this species given that it is the ageing structure of choice and their otoliths are composed of a mixture of calcite and vaterite, which poses challenges for chemical analysis and interpretation (Pracheil *et al.*, 2017). Tzadik *et al.* (2017) investigated elemental and isotope ratio profiles across fin rays of a number of species and found strong concordance in patterns of some constituents between otoliths and fin rays from the same individuals, supporting the utility of fin rays as a non-lethal alternative to sampling otoliths. Lifetime patterns of organic stable isotope ratios ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) were also consistent with known individual histories, suggesting that these structures with higher organic fractions offer additional insight into dietary chronologies that are analytically difficult to obtain from otoliths themselves. Finally, Phelps *et al.* (2017) employed elemental signatures in acipenserid fin rays sampled non-lethally to determine movement of individuals between reaches of large river systems. The use of non-lethal alternatives to otoliths is critical for these types of vulnerable species where mortality must be avoided.

The insights about ecology of mobile fishes derived from chemistry of otoliths and their analogues are valuable, and frequently unobtainable from other tagging or tracking methods. Detailed knowledge about natal origins, habitat use and migratory variability is critical not only for expanded understanding of the ecological roles of a range of taxa, but also for effective management of exploited fishery species. In a survey of the applicability of otolith chemistry studies to fisheries management, Carlson *et al.* (2017) point out that the majority of otolith chemistry publications do not directly discuss the

implications of their data to management. In many cases, this may be because the aim of the study was a specific ecological question that may ultimately have management implications when combined with other species-specific information. Yet, clearly the widespread adoption and advancement of chemical analytical techniques has offered unprecedented insight into the lives of mobile fishes, and the integration of such findings into management strategies will be essential to devise effective approaches to sustain commercial and recreational fisheries.

The frontiers of the field of otolith chemistry are steadily advancing for analytical techniques, statistical methods and applications to novel biogenic structures, species and habitats. Specifically, the continued validation and expansion of potential analytes that can be used to derive information about environmental histories is critical to allow the field to move beyond the realm of salinity and temperature histories alone. Markers for pollution exposure, hypoxia, pH and beyond deserve close attention and experimental verification to fully understand the biotic and abiotic drivers of signature variability in hard parts. Coupled to these efforts should be an increasing focus on physiological controls of elemental regulation, uptake and incorporation into structures. While taxonomically quite different, the careful work of numerous coral geochemists to unravel the complexities within the biotic 'black box' that modifies inorganic dynamics can serve as a valuable model for experimental and modelling approaches for otolith chemists. The coral geochemistry literature is extensive with numerous experimental validations and biochemical modelling of elemental uptake dynamics, and otolith chemists are urged to familiarize themselves with such work to advance their own field more rapidly. In addition, the biochemical processes regulating ion transport across membranes are fundamental for understanding otolith chemistry dynamics. Otolith chemists must also pay careful attention to historical insights and current advances in the biochemistry and physiology realms, particularly given these fields are actively exploring the complexities of ion transport in the face of environmental acidification and deoxygenation. Finally, interest in otolith chemistry techniques has exploded over recent decades, and chemical analysis of fish hard parts is becoming standard in the toolbox of techniques to assess life histories of fishes. With this growth comes an increasing need to ensure that students and new practitioners in the field are properly trained in analytical and statistical techniques as well as a robust understanding of the advantages and limitations of these approaches. The wealth of literature on otolith chemistry is the foundation on which future work rests, and the frontiers cannot be expanded without a thorough appreciation of the historical development of the field. Newcomers to this field are therefore urged to spend considerable time reviewing the experimental and field-based advances and insights gained over recent decades of the published literature when considering future directions. It is in this way that the frontiers of the field will truly be expanded with maximum impact.

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