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Introduction to the 6th International Otolith Symposium

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Fish otoliths have been used as natural recorders of age and growth information in fishes for over a century after the identification of otolith age increments (Reibisch 1899). In addition to measuring age and growth, otolith morphometry has revealed information ranging from taxonomic diversity in contemporary and ancient assemblages, population mixing and evolutionary relationships among species. The analysis of otolith chemistry has also become a method of choice to reconstruct lifetime migration patterns, natal origins and connectivity patterns, environmental histories and trophic interactions in marine and freshwater systems alike. The otolith is thus an invaluable repository of information useful for unravelling questions about demographics, population structure, ecosystem interactions and impacts of environmental stressors. Insights gleaned from otoliths help improve our understanding of ecological dynamics of diverse taxa and inform management practices for artisanal to industrial fisheries worldwide. Many of the analytical methodologies developed for otoliths have been further applied to other calcified structures in aquatic organisms, e.g. scales, bones, statoliths, that provide analogous biological, ecological and environmental information. The International Otolith Symposium (IOS) series has served as a platform for otolith researchers to communicate recent developments and advances starting with the first IOS in 1993 in the US, followed by IOS held in Norway, Australia, USA and Spain, and have been held every 4–5 years. The latest in this series was the Sixth International Otolith Symposium held on 15-20 April 2018 in Keelung, Taiwan, which was the first time an IOS has been convened in Asia. This symposium was hosted by National Taiwan Ocean University and the participants included 234 scientists from 37 countries with a total of 239 oral and poster presentations.

Numerous analytical advances in the field have occurred over the 26 years since the first IOS was held. Otolith research provides insight into various questions; however, some significant knowledge gaps about otolith science still remain, such as the mechanisms of otolith biomineralisation. Five major research themes were identified in the 6th IOS, including (1) Morphology and Physiology, (2) Chemistry and Composition, (3) Sclerochronology and Environment, (4) Life History and Fisheries, and (5) Statistics and Modelling. The use of otolith chemistry as a tool featured not only in the Chemistry and Composition theme, but also appeared in other research themes when relevant to the particular study in question. Walther (2019) reviewed the field of otolith chemistry research, discussed its applications and limitations as an analytical tool, and identified six broad categories of questions that can be investigated with this technique. Identifying origins was one of them, and several studies used novel combinations of analytical approaches to elucidate origins and migration patterns in different taxa. Rogers et al. (2019) explored the early life history of King George whiting (Sillaginodes punctatus) by analysing otolith microstructure and multielement composition of settlement-stage larvae and concluded that different chemical compositions indicated spatial and temporal variation in the origins of populations in South Australia. Stable isotope analyses of both otoliths and muscle tissue were used to trace habitat use of pink ear emperor (Lethrinus lentian) between vegetated lagoons and coastal artificial reefs during ontogenetic migrations, and the authors recommended that multiple nursery habitats along the coastal region should be preserved for population conservation (Le et al. 2019). One powerful otolith isotope marker in freshwater systems is strontium isotope ratios (⁸⁷Sr/⁸⁶Sr) that can distinguish among signatures derived from geologically distinct locations, often at small spatial scales, to support freshwater conservation biology. An isoscape of ⁸⁷Sr/⁸⁶Sr was used to estimate natal origins and adult fish migration patterns of a threatened potamodromous cyprinid (Feyrer et al. 2019). With 100% classification success, Clear Lake hitch (Lavinia exilicauda chi) can be traced back to their natal tributary streams, and individual habitat use patterns over their lifespan were identified. Because some isotope ratios are homogenous in marine environments, artificial spiking of Ba isotopes was used for mass marking the paralarvae of bigfin reef squid (Sepioteuthis lessoniana) to enable origin tracking. Chiang et al. (2019) evaluate the ¹³⁷Ba marking technique in this species and addressed its potential effects on incorporation of other elements when marking. Together these studies showcase the versatility of natural and artificial chemical markers when attempting to identify origins of wild-captured fishes.

As otoliths are chronological recorders of the lives of fishes, conducting transect analyses to obtain chemical profiles across otoliths can be used to assess adult fish migration patterns. Artetxe-Arrate et al. (2019) investigated stock structures of vellowfin tuna (Thunnus albacares) in the Indian Ocean by using combinations of stable carbon and oxygen isotopes along with elemental signatures. Analogous to chemical composition analysis of teleost otoliths, Pistevos et al. (2019) quantified elemental variations in Port Jackson shark (Heterodontus portusjacksoni) vertebrae and found the method was a promising natural tag for tracking its environmental history. As a salinity tracer, the Sr/Ca ratio has been long studied for reconstructing environmental exposure histories for mobile and resident species alike. Tran et al. (2019) use seven elemental ratios to trace salinity histories in the commercially important catfish (Pangasius krempfi) in the Mekong River, with Sr/Ca ratios showing the most suitability as a salinity tracer. The authors concluded that one single freshwater spawning ground was likely given the constantly low levels of Sr/Ca ratios for all fish, but two types of subsequent migration timing patterns were observed. Further increases in analytical methods may broaden the suite of chemical markers that could be assayed and increase spatial resolution of chemical assays across growth increments to reveal fish life-history diversity.

The ability to quantify metabolic rates from chemical markers, such as stable carbon isotope compositions of otoliths, has rapidly advanced in the past decade, and this method holds great promise to reveal fish growth and physiological responses to variable environments. Chung et al. (2019) comprehensively reviewed this technique to illustrate the potential of otolith δ^{13} C as a metabolic proxy that allows otoliths to record individual fish physiology. Godiksen et al. (2019) described the temperature effects on tissue-diet isotopic trophic discrimination factors of nitrogen and carbon in otolith organic matter. Otolith isotopes were then used to reconstruct the trophic position of juvenile cod (Gadua morhua) and found temperature may influence the discrimination factors that could bias trophic-position estimates for fishes living in environments with seasonal temperature variation. Reconstructing dietary and metabolic histories from otoliths is an expanding frontier that has the potential to shed light on a range of ecological questions regarding physiological stressors and trophic interactions.

Age and growth information is important for fishery management, and these variables have been quantified primarily by growth increment measurements. Age validation is essential to assess the accuracy of these techniques. One approach to age validation in otoliths is measurements of ¹⁴C. Andrews et al. (2019) used laser ablation-accelerator mass spectrometry techniques to provide continuous records of ¹⁴C uptake to increase the aging precision of red snapper (Lutianus campechanus). Casselman et al. (2019) also validated age of another long-lived species, lake whitefish (Coregonus clupeaformis) using bomb radiocarbon age validation and found that traditional ageing methods can significantly underestimate ages leading to erroneous natural-mortality estimates. Age estimation may also be attempted by cross comparisons of multiple incremental structures within the same individuals. Shimose and Yokawa (2019) estimated daily age of striped marlin (Kajikia audax) in the tropical eastern North Pacific by comparing otolith

microincrements and dorsal-fin spine sections, and they estimated hatch timing to be earlier than known spawning seasons in other populations. Age validation remains a central requirement for effective interpretation of all forms of otolith-derived data, and these contributions highlight novel approaches to validation.

Population structure is another key concept necessary for effective fishery management, and otolith shape analysis has been used frequently to quantify exchange of individuals among regions. Cerna et al. (2019) investigated stock structure of anchoveta (Engraulis ringens) distributed along coastal waters of Peru and Chile, where juvenile and adult fish from three geographical zones showed significant spatial variation in otolith morphology. Based on otolith-shape analyses, they found that juvenile and adult anchoveta were partially segregated in the northward and southward zones during their life cycle. Such population-structure information is useful for such an important fishery resource in the Humboldt Current system. Cephalopods can exhibit high variability in life-history characteristics, such as longevity and size-at-age, and thus cephalopod statolith daily-growth increments can be valuable growth recorders analogous to otoliths. Jones et al. (2019) described two size-dependent behavioural morphotypes of mature males in Patagonian squid (Doryteuthis gahi). Analyses of age structures of seasonal spawning cohorts suggest the extremely large mature male morph, or 'superbull', arises through phenotypic plasticity and likely provides connectivity as a side effect of body shape and size rather than a genetically selected advantage. Otolith-shape variation can be used also for fish species identification. Lin and Al-Abdulkader (2019) identified fish families and species from the western Arabian Gulf by otolith-shape analysis and discussed factors affecting the identification process. Morphometry of calcified structures will continue to be a useful technique to quantify population mixing and stock structure where identifiable differences among groups exist.

The importance of proper statistical analyses of data derived from otoliths and other structures are of paramount importance to produce accurate estimates of target parameters. For instance, otolith-shape analysis can vary significantly between readers (Aulus-Giacosa *et al.* 2019) and sampling strategies (Chang *et al.* 2019), requiring adequate treatment of variance in models deriving from methods that produce these types of data. Otolith researchers are cautioned to take care in selecting appropriate techniques with sound statistical approaches to make supported conclusions derived from otolith data.

Otolith research continues to develop across many themes, as seen in the presentations at the 6th International Otolith Symposium and contributions to this special issue. The conclusions drawn from research involving otoliths and analogous structures in fishes and other aquatic taxa play important roles in fishery management and assessments of ecological dynamics in marine, coastal and freshwater systems. Future advances in statistical techniques to analyse multi-dimensional datasets that combine chemical, morphological and demographic data from otoliths with additional markers, such as genomic and physiological indicators, will be required to further advance this burgeoning field. Furthermore, studies on the mechanisms of calcification in otoliths could be greatly enhanced by cross-disciplinary work with researchers investigating corals, foraminifera, bivalves and other calcifying organisms or structures. We recommend that future IOS meetings consider inviting relevant researchers outside of the circle of otolith scientists to facilitate crosstaxonomic and interdisciplinary discussions to further advance our understanding of these valuable structures. The next International Otolith Symposium will be held in Chile in 2022.

Conflicts of interest

C.-H. Wang, B. D. Walther and B. M. Gillanders are all guest editors of the International Otolith Symposium special issue and B. M. Gillanders is an Associate Editor for *Marine and Freshwater Research*. Despite these relationships, they took no part in the review and acceptance of this or any other manuscript in this issue that they authored. The authors declare that they have no further conflicts of interest.

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