



Reading the biomineralized book of life: expanding otolith biogeochemical research and applications for fisheries and ecosystem-based management

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Abstract Chemical analysis of calcified structures continues to flourish, as analytical and technological advances enable researchers to tap into trace elements and isotopes taken up in otoliths and other archival tissues at ever greater resolution. Increasingly, these tracers are applied to refine age estimation and interpretation, and to chronicle responses to

environmental stressors, linking these to ecological, physiological, and life-history processes. Here, we review emerging approaches and innovative research directions in otolith chemistry, as well as in the chemistry of other archival tissues, outlining their value for fisheries and ecosystem-based management, turning the spotlight on areas where such biomarkers can

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support decision making. We summarise recent milestones and the challenges that lie ahead to using otoliths and archival tissues as biomarkers, grouped into seven, rapidly expanding and application-oriented research areas that apply chemical analysis in a variety of contexts, namely: (1) supporting fish age estimation; (2) evaluating environmental stress, ecophysiology and individual performance; (3) confirming seafood provenance; (4) resolving connectivity and movement pathways; (5) characterising food webs and trophic interactions; (6) reconstructing reproductive life histories; and (7) tracing stock enhancement

efforts. Emerging research directions that apply hard part chemistry to combat seafood fraud, quantify past food webs, as well as to reconcile growth, movement, thermal, metabolic, stress and reproductive life-histories provide opportunities to examine how harvesting and global change impact fish health and fisheries productivity. Ultimately, improved appreciation of the many practical benefits of archival tissue chemistry to fisheries and ecosystem-based management will support their increased implementation into routine monitoring.

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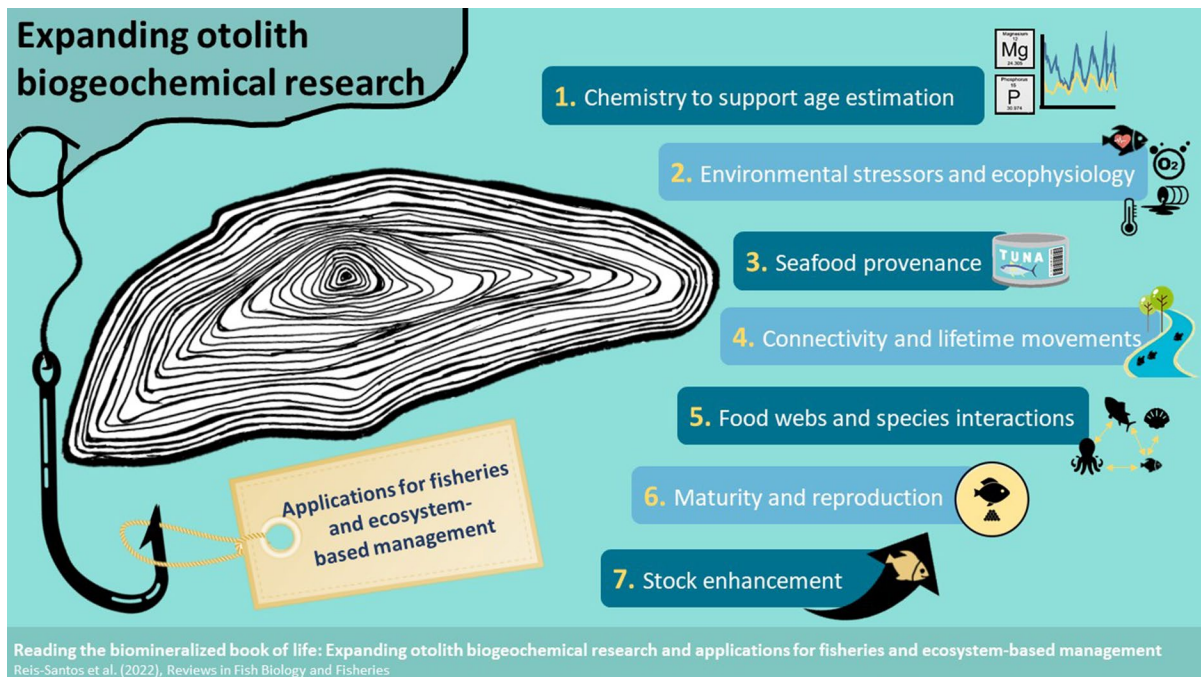
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Graphical abstract



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Introduction

Information extracted from otoliths and other calcified structures is increasingly used to inform sustainable resource management in a rapidly changing world; and such information is often unattainable from sensors, data storage tags or other methods. This is particularly true for early life stages when fish are too small to tag, and otoliths and other archival tissues are used instead as the inert growth layers chronicle each individual's entire life history. As a result, research using otoliths and other archival tissues (e.g., scales, vertebrae, fin rays, eye lenses, statoliths) is growing rapidly. Increasingly, more established techniques such as age, growth and shape analyses are paired with novel chemical approaches to provide new insights into fish life histories, health, population dynamics and demography (Avigliano 2021; Cadrin et al. 2014; Campana 2005; Nazir & Khan 2021; Tanner et al. 2016; Walther 2019).

Otoliths have been at the centre of fisheries science for many decades, but their use has evolved rapidly in recent years, triggered by landmark discoveries,

and analytical and technological advances (Campana 2005; Walther 2019). Chemical analyses traditionally applied to otoliths are now being used on analogous archival tissues such as eye lenses, scales, vertebrae and operculae (Izzo et al. 2016a; Tzadik et al. 2017). While age and growth analyses dominated early otolith research, many recent studies have shown that shape and chemical analyses are powerful approaches to define stocks, reconstruct movements, and unravel individual life histories (Avigliano 2021; Gillanders et al. 2015; Smoliński et al. 2020; Tanner et al. 2016; Tzadik et al. 2017). Importantly, continued advances in analytical techniques have enabled researchers to measure a growing number of elemental and isotopic tracers at increasing fine temporal resolution, allowing them to link adverse environmental conditions to ecological, physiological and life-history processes (Chung et al. 2019b; Heimbrand et al. 2020; Johnson et al. 2020; Reis-Santos et al. 2021; Sturrock et al. 2020). This is a rapidly developing field, and the expansion in research was evident in the “Bio-markers in Calcified Structures” session at the 2021 World Fisheries Congress [Theme 4: Future of Fish

and Fisheries (Innovations in Fisheries)], highlighting the many research directions that can be rapidly translated into fisheries management applications.

As an outcome of this session, we synthesize emerging approaches and major developments in the chemical analysis of otoliths and other archival tissues, outlining their value and pertinence to fisheries and ecosystem-based management, turning the spotlight on areas where such biomarkers can inform fisheries management and support decision making. The current paper does not focus on stock structure [as this has been addressed recently, e.g., Avigliano (2021); Cadrin et al. (2014); Nazir and Khan (2021); Tanner et al. (2016)] but rather reviews recent groundwork on other emerging and innovative research directions, noting areas that are particularly promising for rapid expansion and implementation. Overall, we summarise recent milestones and explore the challenges that lie ahead to using biogeochemical markers in otoliths and archival tissues, grouped into seven application-oriented and interdisciplinary research areas: (1) supporting fish age estimation; (2) evaluating environmental stress, ecophysiology and individual performance; (3) confirming seafood provenance; (4) resolving connectivity and individual movement pathways; (5) characterising food webs and trophic interactions; (6) reconstructing reproductive life histories; and (7) tracing stock enhancement efforts. We focus mainly on otolith research but also draw attention to state-of-the-art research into other archival tissues (e.g., scales, operculae, vertebrae, eye lenses) to highlight synergies and lessons learnt, focusing on the practical benefits of using biomarkers in such structures and next steps to support their application in routine fisheries monitoring.

Chemistry to support age estimation

Age estimation of fish, based on counts of growth increments in otoliths and other archival tissues, underpins calculations of population growth, mortality, longevity. These metrics are fundamental to understanding population dynamics for fisheries assessments and making accurate assignment of ages, which is critical for reliable stock assessments (Hüssy et al. 2016a). However, some species groups (e.g., Clupeiformes and Gadiformes) possess otoliths with diffuse banding patterns, impeding increment

counts. This in turn increases reader subjectivity, leading to poor accuracy and precision for age estimates. Because the periodic formation of growth increments is not ubiquitous among fish, there is a need to validate increment formation, with chemical approaches increasingly explored to overcome issues in growth increment interpretation.

Classic approaches: validation of absolute age

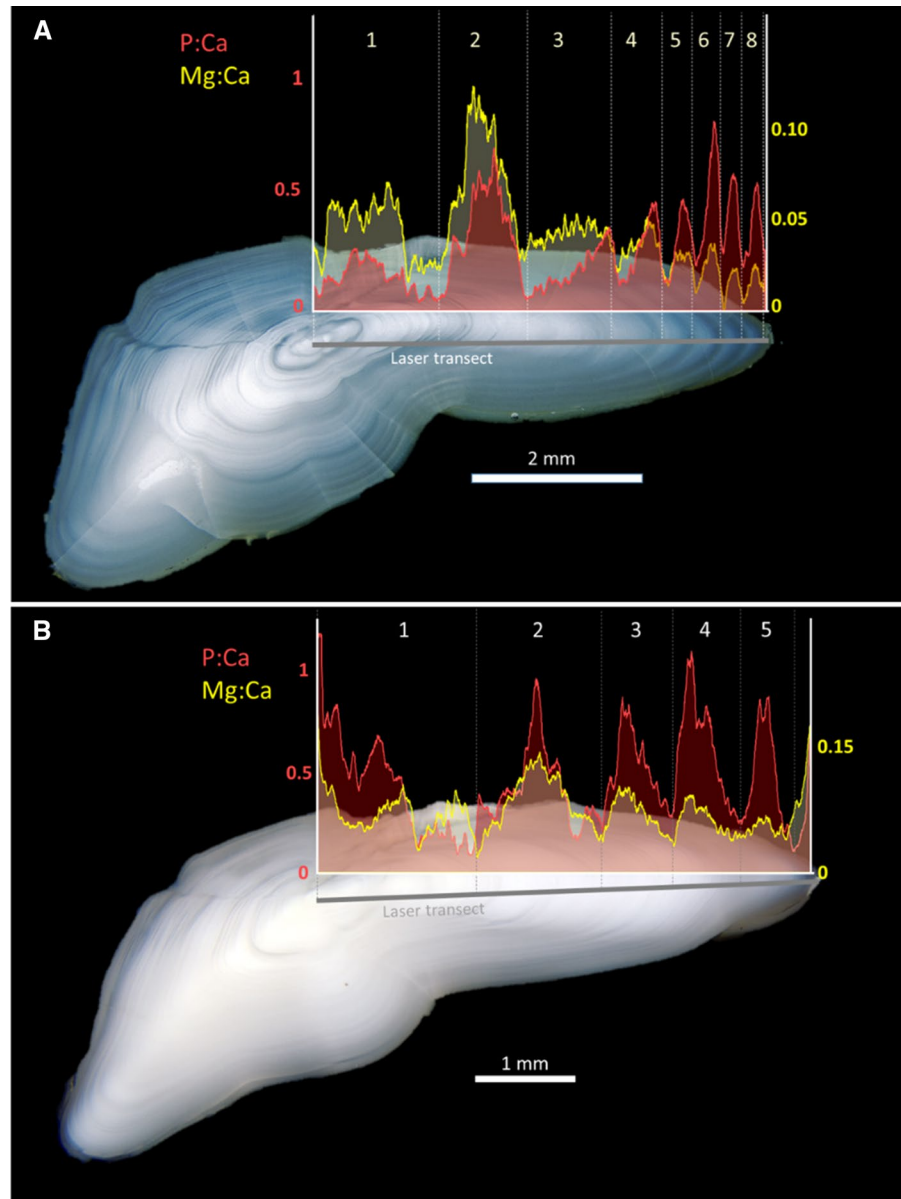
Radiochemical and bomb radiocarbon dating provide indirect chemical methods to validate estimates of the absolute age and growth of fish (Campana 2001). The use of radiochemical methods is based on the uptake of environmental elements and isotopes to otoliths and is particularly useful in long lived species. Radiochemical dating is a geochemical approach that uses naturally occurring radioactivity (e.g., $^{228}\text{Th}/^{228}\text{Ra}$ and $^{210}\text{Pb}/^{226}\text{Ra}$) as a clock within the inert crystalline otolith structure (Andrews et al. 2009, 2012; Andrews 2016; Campana et al. 1993). In contrast, bomb radiocarbon dating uses an anthropogenic radiocarbon signal created by atmospheric testing of thermonuclear devices in the 1950–60s, and their decline over time, as a reference in time relative to ^{14}C concentration levels absorbed by otoliths, or other calcified structures (Andrews et al. 2012; Kalish 1993; Lackmann et al. 2019; Tracey et al. 2017), and can provide absolute ages of individuals depending on their birth year.

Emerging approaches: verification of visual patterns and age estimation

Seasonal patterns in element concentration

Although otoliths are routinely used for age estimation, the formation of ambiguous growth zones can prevent visual interpretation. Accordingly, interest in applying chemical methods for assessing seasonality has increased. One approach to reconstruct seasonal contrasts is temperature-dependent oxygen isotope fractionation (Høie et al. 2004a; Kalish 1991c) in temperate and arctic latitudes (Høie et al. 2004b). To date, oxygen isotope analysis has been used to estimate the timing of growth zone formation in Atlantic cod (*Gadus morhua*) (Høie & Folkvord 2006) and for validating age estimates in Pacific cod (*G. macrocephalus*) (Kastelle et al. 2017). Recently, variations in

Fig. 1 Transverse sections of otoliths of Baltic cod *Gadhus morhua*, and superimposed variations in the chemical composition of P:Ca (red) and Mg:Ca (yellow) from the otolith core to the dorsal edge (measured with Laser ablation ICPMS) demonstrate the usefulness of chemical profiles to support age estimation. **A** is a transverse section of an otolith from an 8-year-old cod from the Baltic Sea, with good readability, associated with clear increments, and high contrast between translucent and opaque zones, that match variations in P:Ca and Mg:Ca. **B** is a transverse section of a 5-year-old cod from the Baltic Sea, lacking clear visual increments, and where oscillations between maxima and minima of the chemical profiles support age estimation where visual increments were unreliable. Dashed lines represent chemical age estimation points and grey lines the laser ablation path. Transverse sections of otoliths were viewed under reflected light (photos: Y. Heimbrand)



chemical concentrations have been explored as tracers of physiological processes to underpin age estimation. Elements P, Mg and Zn are associated with the organic matrix of the otolith (Izzo et al. 2016b; Miller et al. 2006; Thomas et al. 2017) and reflect seasonal variations in growth (Heimbrand et al. 2020; Hüsey et al. 2021a; Limburg et al. 2018) (Fig. 1). Minima often correlate with visually identified translucent

winter growth zones (Friedrich & Halden 2010; Halden et al. 2000; Halden & Friedrich 2008; Hüsey et al. 2016b; Limburg & Elfman 2010) or occur during the coldest months of the year (Hüsey et al. 2021a). Seasonal differences have also been described in Sr (Brophy et al. 2021; Siskey et al. 2016; Tzeng et al. 1999), though this element is often considered a proxy for environmental salinity.

Biological challenges

The key to the successful application of chemical approaches to support age estimation is a detailed understanding of developmental processes and how elements pass various membranes and organs from water and food into the otolith matrix. Tracers of physiology and growth are essential co-factors in many metalloenzymes and are needed for a range of physiological processes, including otolith biomineralization. These interacting mechanisms are complex and hard to tease apart. Even in the well-studied otolith, more knowledge is needed on element uptake dynamics, transport, regulation, and incorporation into the growing otolith crystal lattice to distinguish controlling endogenous and exogenous factors (Hüssy et al. 2021b; Thomas et al. 2017; Thomas & Swearer 2019). In the plasma, elements may occur as free ions (Campana 1999; Payan et al. 2002), protein-bound (P. E. Fletcher & Fletcher 1980; Sturrock et al. 2014) or both. Transport of free ions from plasma into the endolymph is not fully understood and is presumed to occur primarily via passive diffusion along a concentration gradient, whereas elements bound to plasma proteins presumably require active transport across the endolymphatic epithelium. Physiological regulation of element uptake and incorporation is thought to be exerted by a wide range of factors, including ontogeny (Arai et al. 2007; Macdonald et al. 2020; Ranaldi & Gagnon 2010; Reis-Santos et al. 2018b), maturation and spawning (Sturrock et al. 2014, 2015a), diet (Ranaldi & Gagnon 2008), and growth (Hüssy et al. 2021b; Sturrock et al. 2015a) in addition to temperature (Reis-Santos et al. 2013a) which influences metabolic rate, but with considerable uncertainty regarding the magnitude—and even the direction—of the impact on otolith growth and chemistry. It also remains to be seen to what extent uptake mechanisms are universal or subject to phylogenetic differences in incorporation mechanisms (Limburg & Elfman 2010).

Methodological challenges

The ability to detect age-related patterns in chemical composition is determined by the spatial resolution of the analytical method relative to the size and annual growth rate of the archival tissue. The achievable

temporal resolution declines towards the edge of the structure as age increases and growth slows (Høie et al. 2004b; Kestelle et al. 2017). Generally, probe-based techniques [e.g., laser ablation—inductively coupled plasma mass spectrometry (LA-ICPMS)], enable more detailed reconstruction of life histories than methods requiring sample dissolution or combustion [e.g., solution based ICPMS, isotope ratio mass spectrometry (IRMS)]. High-resolution micro-milling followed by IRMS has sufficient resolution to detect temperature related cycles in $\delta^{18}\text{O}$ values in cod up to 6 years of age (Høie et al. 2004b; Kestelle et al. 2017), but long-lived species require higher resolution probe-based secondary ion mass spectrometry (SIMS) (Matta et al. 2010). With LA-ICPMS, continuous line scans can capture oscillations in trace elements at high spatial and temporal resolution allowing for the reconstruction of entire life history profiles (Heimbrand et al. 2020; Hüssy et al. 2016b, 2021a). Alternatively, high-resolution 2D elemental maps, produced using LA-ICPMS (Artetxe-Arrate et al. 2021; Heimbrand et al. 2020; McGowan et al. 2014), particle induced x-ray emission (PIXE) (Halden et al. 2000; Walther & Limburg 2012) or scanning X-ray fluorescence microscopy (Hermann et al. 2016; Tzeng et al. 1999) can reveal spatial heterogeneity in elemental composition, which is useful for observing banding patterns and identifying the optimal transect for analysis of seasonal trends (Heimbrand et al. 2020).

Investigations of age-related patterns in otolith chemistry employ a variety of analytical techniques, including visual inspection of chemical patterns in relation to growth increments (Seyama et al. 1991; Tzeng et al. 1999), statistical comparison of concentrations between opaque and translucent bands (Tomás et al. 2006) and the use of time-series methods to identify peaks or cycles in concentrations (Hüssy et al. 2016b, 2021a; Kestelle et al. 2017; Siskey et al. 2016; Sturrock et al. 2015a). Even with advanced quantitative techniques, the identification of seasonal patterns in chemical data can involve a degree of subjectivity. Standard peak detection algorithms require the user to define the threshold amplitude of a peak and the number of data points (window) over which to search for changes above that threshold (Jarman et al. 2003; Kay 1998). Settings can be optimised with reference to visual bands (Hüssy et al. 2021a) but this requires samples with

clear unambiguous increments and somewhat reduces the independence of the chemistry-based age estimates. Alternatively, spectral analysis methods can detect periodic patterns along a chemical profile and statistically test for annual periodicity; the Lomb-Scargle periodogram is particularly appropriate as it can deal with data that are irregularly spaced (Lomb 1976; Scargle 1982). A potential limitation is the requirement for a temporal reference point, which can be supplied by the position of annual growth marks (Siskey et al. 2016). Nonetheless, even when peaks in elemental concentrations were identified using only visual inspection, inter-reader agreement was higher than with interpretation of visual growth marks for a difficult to age species (Eastern Baltic Sea cod, *G. morhua*) (Heimbrand et al. 2020), indicating that chemical tools can improve the objectivity of age estimation and be a key part in fisheries managers' tool chest.

Two-dimensional mapping of stable isotopes in otoliths is also possible using nuclear reaction analysis (Limburg & Elfman 2017); with further development, this approach could provide a powerful tool for detecting seasonal oscillations and identify spatial patterns in isotope concentration to focus future one-dimensional analyses on. Additionally, further exploration of the periodic table may yield more chemical tracers with applications in novel environments such as deep-sea marine trenches or suboxic environments such as in oxygen minimum zones.

Overview and future directions

Overall, for chemical patterns to be broadly applicable in age estimation, future efforts should be directed towards understanding the mechanisms regulating elemental uptake and incorporation in space and time, validating seasonality of the observed patterns in the field, and identifying statistical methods that provide a more objective estimate of age than the ones used to date. Age estimation based on otolith chemistry is not yet cost-efficient enough to replace traditional visual growth increment reading directly. The approach, however, provides crucial calibration for assessing the accuracy of traditional age readings or size at age information used in length-based assessment models, in particular for species

or populations with ambiguous growth increments. Depending on intended use, cost–benefit analyses will help identify to what extent the use of chemistry-based age estimation is sensible.

Environmental stress and ecophysiology

The use of archival tissues to identify exposure and responses to environmental stressors in aquatic ecosystems is one of the most promising applications of otolith chemistry. Otolith chemistry reflects external and internal processes expressed within a temporal framework. Therefore, variations in otolith tracer composition can indicate the extent, frequency, and duration of exposure to environmental stressors (external influences) as well as aspects of the individual's response to those stressors (internal factors). Such information is valuable for resource managers to disentangle potential exogenous stressors on fish populations (i.e., beyond fishing effects). However, to extract the maximum information from otolith chemical markers reliably, we need a clear mechanistic understanding of the processes underpinning variations in otolith chemistry, whether internal, external or both. We also need to be mindful of the implications of sampling processes, particularly survivor bias. Significant advances have been made towards understanding the relationship between physiology, environmental conditions and otolith elemental proxies for environmental stressors such as hypoxia and selenium toxicity, and for internal tracers such as hormone residues and metabolic rate (e.g., Chung et al. 2021b; Johnson et al. 2020; Limburg & Casini 2019). More progress has been made where the biochemistry underpinning the proxy is well understood and where validation studies have been conducted to provide robust interpretations of observed patterns in nature for particular species and environmental conditions, although experimental evidence for some influences (e.g., temperature and salinity) have been contradictory (Hüssy et al. 2021b; Izzo et al. 2018). The need for specialized validation studies relating environmental conditions to elemental values in otoliths is one of the primary factors limiting broader application of otolith proxies to quantify environmental stressors.

Environmental stressors

Hypoxia

Reconstructing lifetime exposure to low oxygen conditions requires redox-sensitive geochemical proxies that respond to aqueous dissolved oxygen concentrations and are reliably incorporated into biogenic structures such as otoliths. Manganese appears to meet these criteria in many marine, estuarine and freshwater habitats (Limburg et al. 2015). Mn has varying solubility depending on its valency: in basic and oxic settings Mn is present as highly insoluble oxides, whereas in acidic and reducing (anoxic) waters Mn^{2+} ions are relatively soluble and available for biological uptake. In addition to fluxing predictably from organic-rich sediments to overlying waters during deoxygenation events (Lenz et al. 2015), and below aquaculture facilities (Adey et al. 2009), Mn has been categorized as an intermediate acid in otoliths that appears to be strongly driven by ambient water concentration at the time of otolith increment accretion (Mohan et al. 2012; Sturrock et al. 2015a). However, endogenous factors may also impact uptake dynamics given the impact of hypoxia on metabolism and growth rate. Some researchers have proposed accounting for these endogenous impacts by ratioing manganese to magnesium (Mn/Mg) to produce a hypoxia indicator normalized for metabolism (Limburg & Casini 2018), given the hypothesized influence of metabolism on magnesium uptake (Limburg et al. 2018). Other potential otolith-derived hypoxia indicators include iodine (Lu et al. 2010) and $\delta^{34}S$ (Limburg et al. 2015), although further experimental validations are needed.

The use of hypoxia indicators in fish otoliths has expanded in recent years across species and systems to understand the direct and indirect impacts of this growing environmental stressor. This includes quantifying historical shifts in duration and magnitudes of hypoxia exposure in Baltic cod that are associated with worsening fish condition, size, and performance (Limburg et al. 2011; Limburg & Casini 2018, 2019). Conversely, condition and size-at-age do not appear to be strongly affected by hypoxia exposure in the first year of life for Atlantic croaker (*Micropogonias undulatus*) in the Gulf of Mexico (Altenritter et al. 2018; Altenritter & Walther 2019) nor flounder (*Platichthys* spp.) in the Baltic

Sea (Samson 2021), perhaps due to their relatively higher physiological tolerance to hypoxia exposure. However, coupled measurements of otolith Mn and tissue stable isotopes revealed that hypoxia displaces some individual Atlantic croaker from benthic to pelagic food webs, while others remain feeding on benthic prey, leading to an overall expansion of trophic niches for hypoxia-exposed fish (Mohan & Walther 2016; Steube et al. 2021). The complexity of lethal and sublethal effects of hypoxia on fishes and their associated ecosystems are manifold, and the expanding use of geochemical proxies to assess their impacts hold great promise for a more comprehensive understanding of ecosystem level responses.

Contaminants

Aquatic ecosystems are increasingly threatened by human-mediated sources of contaminants (Guédron & Acha 2021; Schwarzenbach et al. 2006). Elevated levels of metal contaminants have been measured in archival tissues such as otoliths, fin rays, and eye lenses, to monitor elevated exposures and corroborate water quality concerns (e.g., Dove & Kingsford 1998; Mounicou et al. 2019; Selleslagh et al. 2016; Sun et al. 2019). Contaminants such as selenium have also been measured in otoliths from several species and systems to evaluate increased exposure. These include polluted lakes in New York, areas downstream of coal mines in British Columbia, and in freshwater and estuarine habitat impacted by oil refineries and legacy agricultural practices (Friedrich & Halden 2010; Johnson et al. 2020; Limburg et al. 2010). Detection of sublethal levels of contaminants in biominerals is a promising approach for diagnosing sources, pathways, and potential for cumulative exposures relevant to aquatic conservation (Barbee et al. 2014; Johnson et al. 2020). Traditional toxicological investigations resolve only recent exposures whereas contaminants deposited in biominerals can be used to track provenance, life stage, and history and duration of exposures over the lifetime of an animal. Ultimately, otoliths allow us to link past sublethal exposures to long term impacts (e.g., suboptimal early growth) and resulting poor quality phenotypes (Barbee et al. 2014). Combining contaminant chronologies with other assessments of fish condition such as growth, deformities, modified behaviours, and stress responses will assist managers

and regulatory agencies in assessing the magnitudes and impacts of contaminants on fishes (Barbee et al. 2014; Bengtsson et al. 1985; Johnson et al. 2020).

Whilst a wide variety of metal contaminants have been measured in both otolith inorganic and organic components of fish from contaminated areas (Hüseyin et al. 2021b; Limburg et al. 2010; Selleslagh et al. 2016), elements such as mercury and other complex chemical compounds have rarely been detected in otoliths, restricting a broader application for some classes of contaminants, in part due to limitations in measuring these compounds with ICPMS approaches. Overall, structures with purely organic matrices such as eye lenses (Dove & Kingsford 1998), or with high organic contents such as scales (Dua & Gupta 2005; Rahman et al. 2018; Sultana et al. 2017) or fin rays (Sun et al. 2019), may show greater promise for diet-based sources of contaminants (reviewed in Tzadik et al. 2017). Ultimately, to advance the application of otoliths as markers of contamination stress in fish, further research is needed relating values in the environment, fish tissues and otoliths. And also on the role of fish physiology in the transport, regulation, and incorporation of environmental contaminants into tissues and the existence of potential non-linear relationships in the incorporation of contaminants, in particular at high environmental concentrations or under stressful conditions (Bendell-Young & Harvey 1986). Nevertheless, otolith chemistry can augment understanding of contaminant histories by its complementary information (e.g., providing location at time of contamination).

Temperature

Marine heatwaves are extended periods of anomalously warm ocean temperatures that can have unprecedented impacts on marine species and major fisheries (Cavole et al. 2016; Sanford et al. 2019; Santora et al. 2020). They are increasing in frequency with one of the most common responses of organisms to warming ocean conditions being a shift in species distributions and/or spawning phenology. Migratory species that use multiple aquatic habitats to complete their life cycle are vulnerable to shifts that can have impacts at multiple life stages [e.g., California Chinook salmon (*Oncorhynchus tshawytscha*) exposed as juveniles to drought conditions and anomalously warm ocean conditions

as adults (Johnson et al. 2017)]. Oxygen isotope compositions ($\delta^{18}\text{O}$ values) in foraminifera, corals and other biomineralising invertebrates are used in paleo-temperature reconstructions because of the predictable, largely abiotically driven temperature-dependent fractionation (Eakin & Grottoli 2006). Similarly, $\delta^{18}\text{O}$ values in otoliths can be used to reconstruct temperature if the $\delta^{18}\text{O}$ of water is known (Weidman & Millner 2000; Willmes et al. 2019).

Advances in microdrilling and probe-based $\delta^{18}\text{O}$ measurements have allowed temperature profiles to be revealed across the lifetime of fishes at high temporal (days to weeks) and thermal (<1 °C) resolution (Hanson et al. 2010; Sakamoto et al. 2019; Zazzo et al. 2006). As temperature regimes in the world's oceans shift with climate change, the ability to track changes in realised thermal exposures of individual animals as well as their distributions will become increasingly important. For fish species that are constrained (e.g., in riverine networks or place holding taxa) and unable to move to optimally suitable temperatures, $\delta^{18}\text{O}$ in otoliths can be used to quantify temperature-dependent mortality, thermal sensitivity of performance and temperatures experienced by survivors. Noting that, warming may increase performance where the ambient temperature is below the ecological thermal optimum for the species or population. Chemical thermometry of biomineralized tissue should also be compared to optical properties of otoliths for additional information, as daily increment formation is highly sensitive to temperature (Volk et al. 1999). Continued laboratory studies are necessary especially for species living close to their thermal limits since there is some evidence that growth rate, otolith precipitation rate, and metabolic effects could influence oxygen isotope fractionation (Darnaude et al. 2014; Storm-Suke et al. 2007).

Ecophysiology

Individual fish respond to changes in the external environmental conditions through behavioural modifications, physiological responses, and/or changes in performance. The nature and extent to which these responses are expressed reflects an interaction between the individual phenotype and the local environmental and ecological context. Consequently, laboratory-based studies of fish

responses to external environmental drivers may have limited predictive power in complex field settings. There is therefore an urgent need for retrospective measures of fish responses to observed environmental stressors.

Otolith and other archival tissues have relatively untapped potential to reconstruct fish responses to external environmental drivers. For instance, stress responses are coordinated through the endocrine system: the expression of hormones (such as cortisol) in body tissues, including incrementally grown tissues, can indicate triggering of systemic responses to an external stressor. Similarly, an animal's field metabolic rate reflects the sum of energy consuming processes and therefore acts as a holistic record of performance in response to the external environment. Variations in mass-specific field metabolic rates in response to changes in the external environment may indicate the relative sensitivity of whole animal performance to that perturbation. Below we briefly review the state of the art in approaches to recover markers of physiological responses to external environmental and ecological conditions.

Stress hormones

Several studies have demonstrated that exposure to stress causes an increase in the concentrations of cortisol in fish scales (Aerts et al. 2015; Laberge et al. 2019) at levels that are proportional to plasma concentrations (Carbajal et al. 2019). Exposure to temperatures outside of a species' optimal range can activate the hypothalamic-pituitary-interrenal (HPI) axis, thereby inducing an endocrine stress response, which elevates systemic cortisol and is recorded in the scale (Hanke et al. 2019). Scale cortisol has therefore been proposed as an ideal biomarker for monitoring stress responses to climate change for fishes (Goikoetxea et al. 2021). See section Maturity and Reproduction, for more details on links between stress and reproductive hormones on archival tissues.

Metabolic rate

Responses of individuals to external conditions typically have an energetic expression, through changes in behaviour (e.g., energy partitioning) or changes in the availability or accessibility of resources. Estimating total energy use (field

metabolic rate, FMR) is one way to understand how marine organisms respond to environmental pressure and changes. Field metabolic rate has been extremely challenging to determine, especially in aquatic organisms (Treberg et al. 2016). It has long been known that stable carbon isotope values ($\delta^{13}\text{C}$) recorded in biogenic carbonates are not in equilibrium with external waters, and that this disequilibrium reflects contributions from metabolic (respiratory) carbon. Metabolic carbon has much lower $\delta^{13}\text{C}$ values than ambient dissolved inorganic carbon, so increased contributions of metabolic carbon to the biomineralising fluid result in lower $\delta^{13}\text{C}$ values in the biomineral. This process was first identified in foraminifera (Berger et al. 1978) and then widely among marine organisms (e.g., Kalish 1991a; McConnaughey et al. 1997; Solomon et al. 2006). In most biogenic carbonates, the carbon forming the biomineral is dominated either by the ambient or the metabolic source. In fish otoliths (but also cephalopod shells and to a lesser extent bivalves), both carbon sources typically contribute more than 10% of the total carbon in the blood, so that the relative proportion of metabolic compared to ambient carbon provides an analytically tractable proxy for variations in metabolic rate (Chung et al. 2021a; McConnaughey et al. 1997). Otolith $\delta^{13}\text{C}$ values have been applied to infer relative metabolic rates of teleosts in relation to their life stages, functional behaviours, and experienced temperatures (Dufour et al. 2007; Sherwood & Rose 2003; Sinnatamby et al. 2015).

In a further development, experimental work has validated a direct relationship between the proportion of metabolic carbon in the otolith $\delta^{13}\text{C}$ and fish respiratory rates manipulated through ambient temperature (Chung et al. 2019a, 2019b). Establishing this statistical calibration between the otolith isotope proxy for FMR and oxygen consumption rate extends the use of the otolith metabolic proxy in broader ecophysiological research. A key advantage of using otoliths as proxies of field metabolic rate is that the analysis required to obtain $\delta^{13}\text{C}$ values also returns $\delta^{18}\text{O}$ values. Each otolith sample therefore provides an estimate of the time-averaged temperature experienced by the individual fish and the time-averaged field metabolic rate expressed at that temperature. Combined with body size data, this allows insight into thermal sensitivity and allometric

scaling of FMR as well as identifying conditions (i.e., stressors) where field metabolic performance is reduced, providing added value to routine monitoring (Alewijnse et al. 2021; Chung et al. 2021b; Smoliński et al. 2021).

Mortality/selection

Environmental stressors in aquatic systems such as warming water, hypoxia, and pollutants often cause direct or latent mortality to individuals with often unquantified impacts to populations. Selective mortality during early life stages can have significant population-level consequences, yet critical periods when selective mortality occurs, the strength of selection, and under what environmental conditions, can be difficult to identify (Garrido et al. 2015; Sinclair et al. 2002). Otoliths and archival tissues are ideal structures to assess the magnitude of survival bias (mortality) through cohort-based sampling. Age reconstructions in fisheries have revealed poor recruitment of particular year-classes and growth variability due to environmental fluctuations or extreme events that may result in fish kills (Martino et al. 2019; Pinto et al. 2021; Reis-Santos et al. 2021; Wang et al. 2011). Similarly, Woodson et al. (2013) reconstructed daily growth rates in Chinook salmon from cohorts through time and demonstrated that individuals that were larger and growing faster during their early lives had greater survival than smaller and slower growing individuals during poor oceanographic conditions. Additional monitoring data can be particularly powerful when paired with otolith reconstructions to estimate the strength of selection for particular traits such as fish size, growth, or migration timing as a function of environmental conditions (Martino et al. 2019; Sturrock et al. 2015b, 2020). For example, Sturrock et al. (2015b, 2019) used routine monitoring data of fish sizes collected from juvenile Chinook salmon leaving rivers and compared them to reconstructed fish sizes at emigration using Sr isotopes in the otoliths from surviving adults from the same year-classes. This work quantified size-selective mortality as a function of hydrologic condition and identified water release strategies from reservoirs to support a portfolio of outmigration behaviours in salmon (See section: Connectivity and Movement Reconstructions Across Life-stages). A similar approach can be used linking

water temperatures and fish distributions at early life stages and temperature-dependent mortality reconstructed from survivors in that cohort using $\delta^{18}\text{O}$ in otoliths. Conversely, consistent observed chemical patterns over time may indicate a lack of stress-selective mortality. For instance, Altenritter and Walther (2019) used multivariate analyses of otolith chemical proxies of hypoxia exposure patterns during the first year of life (e.g., duration and magnitude) and found that exposure patterns of surviving Atlantic croaker did not change significantly over time. Thus, this species appeared to be relatively tolerant to hypoxia exposure, at least for the life history stages that were sampled. Future efforts should aim to explore shifts in demographic metrics recorded in archival tissues linked to landscape scale environmental stressors.

Overview and future directions

Overall, chemical tracers in biomineralised tissues of fishes have been used to infer aspects of the external environment such as water temperature, pollutant exposure, or hypoxia. However, alteration of biomineral chemical composition based on internal processes, or retention of metabolites or hormones within the biomineral provides a concomitant signal to infer physiological responses to the external environment. Biomineralised tissues can therefore offer a simultaneous record of the change in the external setting, together with a record of the physiological and/or behavioural response to that stressor, all within a temporal context offered from the incremental nature of the tissue. Furthermore, by working retrospectively using tissues collected from free-swimming wild fish, we record the realised effects of a stressor on individuals after they have taken whatever mitigation actions are available to them within the specific ecological/environmental context. Identifying responses that cannot be behaviourally mitigated or that are overcome at physiological cost is arguably more ecologically relevant and more pertinent to management than determining lethal limits in laboratory contexts.

All biomarker approaches described here can provide more information when used in combination with other biomarkers, including tagging and gene markers. In combination such data will make significant progress in validating and evaluating individual responses to environmental pressures, like

warming, hypoxia, harvesting on fish and fisheries. However, it is important to note that studies drawing on retrospective analysis of biomineralised tissues recovered from live caught individuals commonly suffer from survivor bias. One remedy will be to track early life cohorts occurring in stressed environments, taking advantage of daily growth increments to track mortality in combination with chemical information. In the context of environmental stressors, sampling natural mortalities and/or animals in poor condition is important, but may be complicated where a lack of growth reduces accretion of the biomineralised tissue.

Seafood provenance

A significant challenge for fisheries management and the seafood industry is to accurately pinpoint the harvest location of seafood products (used here in its

broadest sense to encompass both freshwater, estuarine and marine products). Unlike most food commodities, many seafood products are sourced from wild populations, where high seas transshipping and processing operations allied to complex and obscure supply chains make it increasingly challenging to trace product origin, and provide a backdrop for illegal and fraudulent activities (Fox et al. 2018; Kroetz et al. 2020; A. J. Silva et al. 2021). In this context, seafood provenance and forensics is an emerging area of research driven by the growing recognition that malpractices undermine sustainable fisheries, erode management and conservation efforts, and pose potential risks to consumer health (Fonseca et al. 2022; Leal et al. 2015; A. J. Silva et al. 2021).

Provenance (i.e., the geographic area of collection or production of seafood), together with product authenticity (i.e., a product is genuine regarding species, wild vs farmed, or location of origin) and

Table 1 Examples of using biomarkers in calcified structures for seafood provenance applications

Structure	Taxa	Chemical marker	Analytical method	References
Statolith	Octopus (<i>Octopus berrima</i>)	Multiple trace elements	laser ablation ICPMS	(Daryanani et al. 2021)
Statolith	Octopus (<i>Octopus berrima</i>)	O and C isotopes (combined with multiple trace elements in soft tissue)	IRMS	(Martino et al. 2021)
Shell	Goose barnacle (<i>Pollicipes pollicipes</i>)	Multiple trace elements	solution based ICPMS	(Albuquerque et al. 2016)
Shell	Scallops (<i>Pecten maximus</i>)	Multiple trace elements (combined with multiple trace elements in soft tissue)	solution based ICPMS	(Morrison et al. 2019)
Shell	Cockles (<i>Cerastoderma edule</i>)	Multiple trace elements	solution based ICPMS	(Ricardo et al. 2015)
Shell	Mussel (<i>Mytilus edulis</i>)	Multiple trace elements (combined with multiple trace elements in soft tissue)	solution based ICPMS	(Bennion et al. 2019)
Shell	Cockles (<i>Cerastoderma edule</i>), Clams (<i>Ruditapes decussatus</i> , <i>R. philippinarum</i>)	Multiple trace elements	solution based ICPMS	(Mamede et al. 2021)
Otolith	Freshwater fish (<i>Arapaima spp.</i>)	C and Sr isotopes	IRMS (C) Laser ablation MC-ICPMS (Sr)	(Pereira et al. 2019)
Otolith	Marine Fish (<i>Dicentrarchus labrax</i> , <i>Sparus aurata</i>)	Multiple trace elements	solution based ICPMS	(Arechavala-Lopez et al. 2016)
Scales	Diadromous fish (<i>Salmo salar</i>)	Multiple trace elements	solution based ICPMS	(Adey et al. 2009)

traceability (i.e., means to follow a product along the supply chain) are straightforward concepts and key components in seafood, fishery and aquaculture regulations (e.g. EU, No 1379/2013), but their implementation requires effective tools for testing and verifying information (Carter & Chesson 2017; Cusa et al. 2021; Gopi et al. 2019a). Therefore, capitalizing on the intrinsic properties of calcified structures and their chemical composition provides an opportunity to develop systems to validate seafood provenance. In doing so, we are empowering managers to safeguard legal and sustainably managed fisheries, as well as guarantee compliance and the legitimacy of certification programmes (Armenta & de la Guardia 2016; Leal et al. 2015).

Chemical and isotopic composition in calcified structures such as otoliths or bivalve shells have long been used by fishery scientists and ecologists to inform stock or management units (Albuquerque et al. 2016; Avigliano 2021; Tanner et al. 2016), and discriminate habitat use at small and large scales (see Section on Connectivity and references therein). These intrinsic markers have the advantage that all individuals are naturally marked, reflect geographical conditions mediated by variations in the surrounding environment (e.g., water chemistry, salinity, temperature) (Campana 1999; Izzo et al. 2018; Reis-Santos et al. 2013a), and therefore can also underpin provenance assessments. Critically, calcified structures allow retrospective analyses through the lifetime of the individual that can be used for more detailed assignments among locations, or a potential tracer for interventions during aquaculture [e.g., changes in rearing conditions (salinity, hypoxia, feed, other treatments), mass-markings for origin identification]. Despite these benefits, the application of natural chemical markers in calcified structures specifically for seafood provenance is surprisingly minimal (see Table 1). Furthermore, of the known examples, few studies have used LA-ICPMS (Daryanani et al. 2021; Pereira et al. 2019), even though this is by far the leading analytical method used by ecologists to analyse the trace element chemistry of biominerals. Compared to solution based ICPMS or IRMS of soft and hard tissues that dominate seafood provenance research and where samples are digested in acid before analysis (Cusa et al. 2021; Gopi et al. 2019a, 2019b), LA-ICPMS has minimal sample preparation, low contamination

risk, and allows precise analytical spatial resolution of a large number of samples. Whilst instrument availability still varies across the globe, these traits have made LA-ICPMS routine outside the seafood provenance field, and we should capitalize on its high throughput to shift the current model and advance the implementation of LA-ICPMS to speed up response times for regulators aiming to safeguard compliance but also claims on geographic origin.

Provenance assessments based on otolith chemistry are to date centred in distinguishing wild versus farmed seafood products (Arechavala-Lopez et al. 2016; Pereira et al. 2019) (Table 1). In this case, both studies successfully trace back wild and farmed fish from different origins, with Pereira et al. (2019) also combining the use of radiogenic markers ($^{87}\text{Sr}/^{86}\text{Sr}$) and $\delta^{13}\text{C}$ from otoliths to discriminate provenance of freshwater fish along a large expanse of the Amazon. While we acknowledge there are other otolith studies that could be usefully applied to the question of seafood provenance (e.g., Gillanders & Joyce 2005; Johnson et al. 2012) we limited Table 1 to studies that directly address seafood provenance. Considering other calcified structures, recently, the chemical composition of octopus statoliths demonstrated these are a powerful tool to track the provenance of octopus at regional/domestic and international scales (Daryanani et al. 2021; Martino et al. 2021). Scale chemistry has also identified wild versus farmed salmon (Adey et al. 2009). But, thus far, bivalve shells are the most commonly used calcified structure to assess provenance, where chemical composition can reveal harvest period (Morrison et al. 2019) and has shown incredible spatial resolutions (down to 1 km apart) (Ricardo et al. 2015), with the influence of harvest location strong enough to overcome species-specific variability and allow the use of species as proxies of others (Mamede et al. 2021).

Building reference libraries of geographical locations of interest is key to the successful application of otoliths and other calcified structures to test if particular geographic claims are true. Alternatively, spatial models of chemical variation can be developed (e.g., isoscapes or maps of elemental variation), ideally encompassing seasonal or other temporal variations (Cusa et al. 2021; Gopi et al. 2019a) (like in connectivity and movement reconstructions, see respective section). Such baselines boost the certainty of the retrospective

assignment of seafood provenance and legitimise managers and regulatory agents to support sustainable and well-managed fisheries, but also underpin denomination of origin programmes, identify wild versus farmed, or discriminate sources of aquaculture products. While in need of further development, portable X-Ray Fluorescence (XRF) could also be a game changer enabling real-time, on site, forensic applications for seafood provenance.

Provenance testing can be framed as a set of questions with increasing requirements in terms of reference data and assumptions (Cusa et al. 2021). The simplest type of question requiring the least additional data can be framed as:

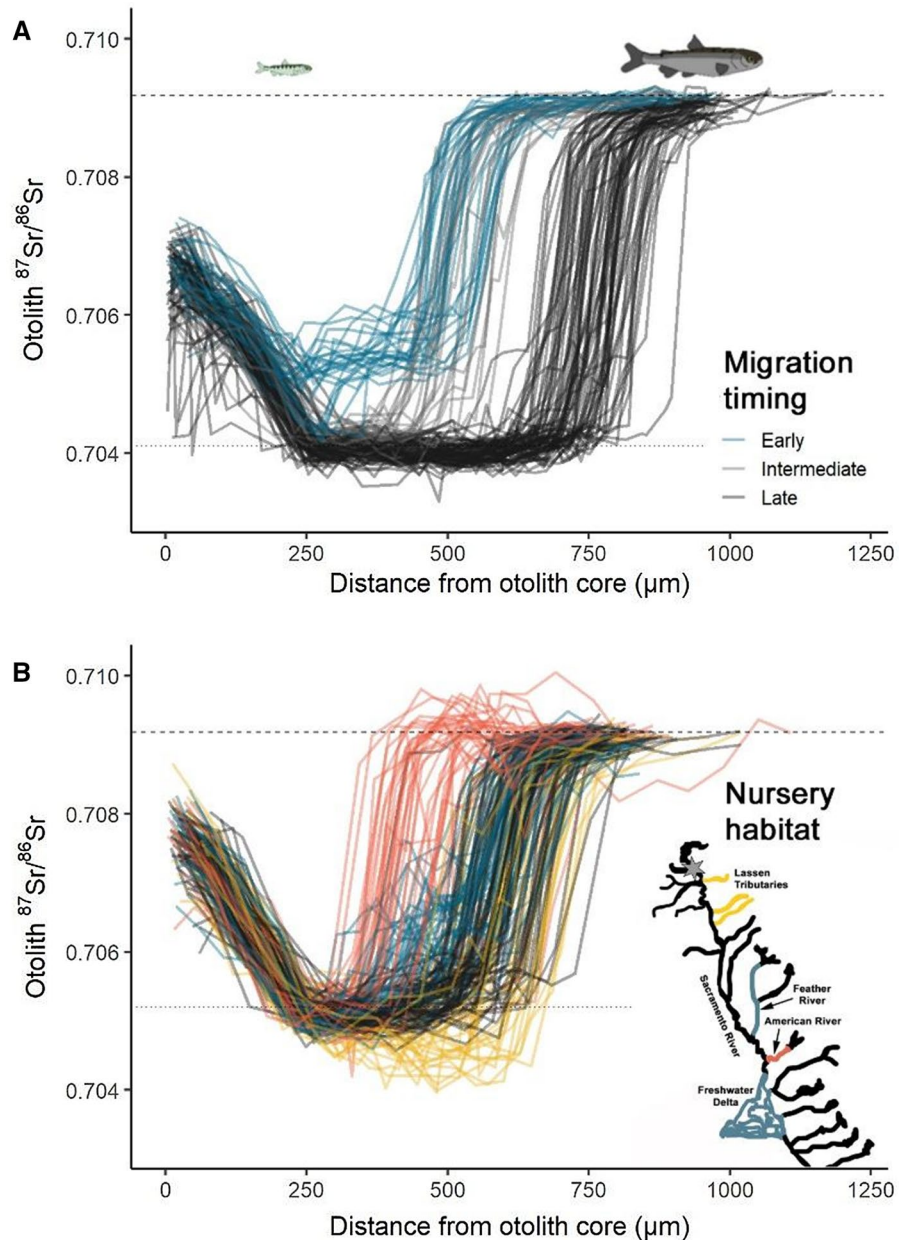
- (1) Is the test sample consistent with coming from a specific, spatially restricted, and known place? In this case, the sample design requires testing against reference data or estimates of the chemical matching that of the claimed origin, with the spatio-temporal scale of the reference data ideally matching that of the claimed origin. Note that matching consistent patterns may not always indicate origin, as there is potential for unsampled regions to also match – but identifying mis-matching tracers can demonstrate that a claimed origin is unlikely.
- (2) Which of a set of discrete sites is the most likely origin? This question is an extension of the above, simply requiring additional reference datasets capturing the likely tracer composition among sites. Addressing the question adds extra sample complexity as each potential origin site should be characterised with equal efficiency in the reference. Noting that the effective likelihood of assignments to any site is likely to reduce as the number of candidate sites increases – therefore choice of candidate sites is important.
- (3) Where did the test sample likely come from? This is by far the most challenging application, as it requires complete characterisation of all possible origin areas. Successful applications of biomarker approaches to unconstrained provenance problems are likely to be limited to broader questions (e.g., comparing temperate

to tropical origins, distinguishing wild from farmed).

In all three of these cases, demonstrating the accuracy of the approach can be challenging. Assignment accuracy is often estimated by subsampling the population used to create a reference dataset and assessing the likely origin of that subsample using decision rules built from the reference population. Clearly in this case the reference and test populations are not independent, and estimates of assignment accuracy are estimates of maximum possible assignment accuracy. There are very few examples in the seafood provenance (but also stock structure or connectivity) literature where geographic assignment accuracy has been estimated using genuinely independently-collected datasets (Cusa et al. 2021).

Although the use of natural biogeochemical tracers in seafood provenance is increasing, most of these applications draw on the chemical composition of organic tissues. This is understandable where seafood products are traded as processed, and whereby calcified structures are typically removed. However, when calcified tissues are retained (e.g., whole seafood or partially processed seafood) they are a formidable tool for establishing provenance. A major advantage of otoliths and other calcified structures for provenance assessments is that the natural chemical markers are tamper resistant, as they are permanently locked in the calcified matrix, and collections to develop reference libraries can be easily compiled, as these samples can be stored dry for decades, with minimum maintenance. Importantly, otolith collections are widely available, as otoliths are routinely used in global fisheries assessments, and can be collected at the point of landing (often without decreasing product value) or throughout the supply chain in specimens that are traded whole. Yet, existing monitoring programmes and otolith repositories remain underutilised for provenance assessments and to build reference libraries or maps of chemical variation. Ultimately, otoliths and calcified structures are an untapped resource that can enable the development of a clear and easy to implement framework to underpin compliance and food labelling laws by identifying the geographical origin of wild and farmed seafood.

Fig. 2 Life history diversity of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in the California Central Valley revealed by otolith strontium isotope profiles measured in the otoliths of post-spawned (i.e. 'successful') adults, emphasizing **A** the temporal diversity in emigration timing of spring run salmon (both from their natal river and into the ocean), and **B** the spatial diversity exhibited by nomadic winter run, which exhibit frequent stop-overs in non-natal tributaries on their way to the ocean (habitat colours indicated on inset map). The mean isotopic value of each population's natal river and the ocean are indicated by short and long dashed horizontal lines, respectively. In **B** the spawning area is indicated by a star and black profile lines indicate fish that reared exclusively in the natal river. Data used with permission from **A** Cordoleani et al. (2021) sourced from <https://doi.org/10.5061/dryad.bk3j9kdc9> and **B** Phillis et al. (2018)



Land-sea connectivity and lifetime movement reconstructions

Maintaining connectivity and life history diversity in freshwater and diadromous fishes

To cope with climate change and increasing population demands, water infrastructure and hydropower developments are rapidly increasing world-wide (Winemiller et al. 2016). These developments have

the potential to further fragment and simplify freshwater and estuarine habitats and threaten the migratory pathways of fishes (Silva et al. 2018). Understanding the potential impacts of planned and future infrastructure is critical to address the practical challenges of river development and to protect feeding, spawning and dispersal habitats (Hall et al. 2011). Traditionally, it was thought that migration pathways were mostly important for adult fish (Gillanders et al. 2015). But recent research has identified that

movement among habitats is important from eggs-to-adults (Grüss et al. 2011). For instance, eggs and/or larvae may have extended drifting periods across many kilometres (Lechner et al. 2016). Juveniles are known to migrate significant distances both upstream and downstream to access critical habitats. Adults might perform spawning or feeding migrations. It is important to understand the movement requirements of each life stage if fish are to be protected across their entire life across river watersheds (Northcote 1984) but also land- to seascape for diadromous species. Furthermore, maintaining inter and intra-specific diversity in life history pathways and timings (e.g., contingents or portfolios of migratory strategies, Fig. 2) allows fish to respond to changing environmental conditions and is critical for resilient fisheries and ecosystems (Des Roches et al. 2021; Moore et al. 2014; Schindler et al. 2010). This requires quantifying individual fish movements among different habitats and across all life-stages.

Otolith analyses have provided unique insights into the spatial and temporal scales of fish migrations, revealing diverse migratory pathways and allowing the categorisation of associated life-history traits (Campana 2005; Cordoleani et al. 2021; Starrs et al. 2016). In some cases, the spatial scale of migration can be vast, and otolith chemistry has been particularly useful, for instance, in identifying diadromy. This is due to substantial chemical differences between marine and freshwater environments, defined by salinity gradients, and their incorporation into the otolith structure which is typically expressed as the ratio of strontium or barium to calcium (i.e. Sr:Ca or Ba:Ca) (e.g., Elsdon et al. 2008; Gillanders et al. 2015; Walther & Limburg 2012). Migrations that occur solely within freshwater require a different approach, and changes in otolith $^{87}\text{Sr}/^{86}\text{Sr}$ ratios can represent movements of individuals between isotopically distinct regions (Barnett-Johnson et al. 2008; Hegg et al. 2013), including within and among rivers (Brennan et al. 2019a; Hermann et al. 2021; Humston et al. 2017; Tran et al. 2021; Walther & Limburg 2012). This latter approach has recently revealed exceptionally long-distance migrations (>8000 km) by goliath catfish (*Brachyplatystoma rousseauxii*) in the Amazon Basin, including natal homing (Duponchelle et al. 2016).

In many cases, the combination of multiple geochemical tracers can be used to enhance the life

history information gained from otoliths (Avigliano et al. 2021; Crook et al. 2016; Macdonald & Crook 2010). For example, using $^{87}\text{Sr}/^{86}\text{Sr}$ ratios alone Duponchelle et al. (2016) were unable to demonstrate natal homing to the upper Amazon River due to less distinct environmental gradients. A follow up study undertaken by Hauser et al. (2020) used Sr:Ca and Se:Ca ratios to confirm natal homing to both the Madeira and Amazon rivers. The large spatial scale of these movements highlights the complexities of fisheries management, particularly where movements cross international borders (Cooke et al. 2012). While otolith chemistry has been instrumental in quantifying the spatial scale of movements, including highlighting long-distance migrations, it has also identified fine scale movements and substantial variability in life-history traits within species. For example, Bell-Tilcock et al. (2021) showed that otolith and eye lens $\delta^{34}\text{S}$ values could be used to reconstruct movements between main channel and floodplain habitats. Phillis et al. (2018) used otolith $^{87}\text{Sr}/^{86}\text{Sr}$ ratios to show the importance of short excursions into small tributaries along the main migratory corridor, demonstrating the importance of maintaining an interconnected riverscape (Fig. 2). Many species exhibit phenotypic variability in migratory tendencies and a single stock can be comprised of multiple contingents, often including both residents and migrants (Chapman et al. 2012a; Secor 1999). Termed partial migration, the prevalence of this phenomena is increasingly being identified through the application of otolith chemistry in freshwater, estuarine and marine environments including across salinity gradients (Chapman et al. 2012b; Gillanders et al. 2015; Hobbs et al. 2019). Finally, otolith chemical analyses have uncovered complex life history portfolios across many different fish species and ecosystems which have implications for management strategies (Brennan et al. 2019a; Hegg et al. 2015; Hodge et al. 2016; Schindler et al. 2010; Vu et al. 2022). Therefore, only by embracing approaches that quantify individual fish movements within populations can we protect ecological heterogeneity and the critical habitats supporting our fisheries. Fisheries and habitat management should consider a holistic approach that recognises that diverse migratory strategies are an integral component of functional land-seascapes and key to safeguarding population resilience and fisheries stability. The future challenge is to link plasticity in individual fish

movements to population-level outcomes, requiring innovative data analysis approaches that maximise the information stored in otoliths to reveal both population connectivity but also the factors driving individual variation in migration pathways, timing and survival (see also Food Webs section).

Linking individual movements with growth and size information

Otoliths' time-keeping properties allow linking chemical measurements with daily and annual growth rings to reconstruct the age and timing of individual movements, as well as habitat or region-specific growth rates (see also Environmental Stress and Ecophysiology). Several recent studies have combined otolith age, growth and elemental or isotopic measurements to demonstrate the importance of divergent movement strategies under varying climatic conditions and differences in growth performance among phenotypes and habitats (Barrow et al. 2021; Cordoleani et al. 2021; Gillanders et al. 2015). In freshwater systems characterized by sharp changes in geology, otolith $^{87}\text{Sr}/^{86}\text{Sr}$ ratios have the potential to reconstruct individual migration pathways at spatiotemporal resolutions comparable to acoustic and data storage tags (Phillis et al. 2018). Emerging time series analyses such as space-time isotope models (Brennan et al. 2019b) and Dynamic Time Warping (Hegg & Kennedy 2021) are increasing the sophistication of such analyses. Such detailed life history reconstructions provide unique opportunities to reveal the impact of specific management actions, such as whether habitat restoration or reservoir releases resulted in appreciable changes in growth, or whether pulse flows cued fish movement (Sturrock et al. 2015b, 2020). Even without time-consuming microstructural analyses, the positive relationship between otolith size and fish size (usually particularly reliable for early life stages) means that the relative growth obtained in different habitats can be estimated (Brennan et al. 2019a, 2019b). Thus, by reconstructing the life of a fish from egg to adult, we can better-understand migratory pathways and provide these data to inform policy decisions and reduce the impacts of future developments across the land-sea interface.

While fine scale movement and growth reconstructions have typically been applied in freshwater systems

or between fresh and marine environments due to larger chemical gradients and thus higher spatiotemporal resolution, there are also applications for fully marine species. For example, growth, movement, thermal and metabolic reconstructions in marine fishes using otolith microstructure in tandem with $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values is gaining traction (Chung et al. 2019b; Sakamoto et al. 2019; Trueman & St John Glew 2019) with finer sampling and detection capabilities through SIMS (Hanson et al. 2010) and new micromilling techniques (Sakamoto et al. 2019) increasing the spatiotemporal resolution possible (See also Environmental Stress and Ecophysiology).

Natal origin, and estuarine and coastal nursery contributions

Many marine fish species use spatially segregated habitats over their life cycle, connecting spawning and nursery areas via pelagic larval dispersal (Cowen & Sponaugle 2009), and juvenile nursery areas and adult populations via recruitment (Beck et al. 2001). Understanding and quantifying these connectivity links is key to assess population structure and dynamics, and to identify important areas and pathways for dispersal and movement, thus providing essential information to ensure management at biologically relevant spatial scales (Gillanders 2002b; Kerr et al. 2016; Phillis et al. 2018; Reis-Santos et al. 2018a). Once more, otolith chemistry provides a unique and versatile approach to identify and quantify connectivity patterns between different life stages of fish, enabling managers to adopt and support fishery and habitat protection decisions.

The pelagic larval stage that connects spatially segregated spawning grounds and nursery areas is heavily influenced by physical processes allowing for large-scale dispersal and connectivity between populations. Yet, evaluating connectivity during the larval stage is initially dependent on the ability to discriminate between individuals from different spawning grounds. This can be achieved by analysing the elemental chemistry of otoliths collected from developing embryos and recently hatched larvae in both marine (Brophy et al. 2003; Rogers et al. 2019; Schaffler et al. 2009; Tripp et al. 2020) and freshwater environments (Barbee & Swearer 2007; Lazartigues et al. 2018). Subsequently, the elemental signatures for each spawning ground can be compared to the

natal signatures of juveniles collected from nursery areas to establish larval connectivity and quantify the relationships between specific spawning grounds and nursery areas (Shima & Swearer 2016; Walther & Thorrold 2010). Because elemental signatures and dispersal patterns can change over multiple temporal scales (Avigliano et al. 2018; Gillanders 2002a; Reis-Santos et al. 2012), it may be necessary to repeat studies, or build libraries of chemical signatures over multiple years to understand variability in dispersal and subsequent recruitment to nursery areas (akin to building reference libraries to test Seafood Provenance). An alternate approach is to simulate dispersal using biophysical models (Swearer et al. 2019). The biological component of these models describes the ontogenetic development of the larvae, which can be retrospectively determined from the otolith microstructure of settled juveniles (i.e., spawn date, growth rate, settlement date) (Rogers et al. 2021; Vaz et al. 2019). Furthermore, the simulated patterns of larval dispersal can be compared to the relationships identified from otolith biomarkers to assess model predictions and best interpret connectivity.

Estuarine and coastal areas are often cited as important nursery habitats (Beck et al. 2001; Gillanders et al. 2003). Juvenile fish recruit into the sheltered estuarine habitats settling in structured habitat such as seagrass, mangroves or saltmarsh where there can be abundant food and reduced numbers of predators. At larger sizes and ages, they then move out to coastal habitats including reefs. In some cases, fish can recruit to both estuarine and reef habitat as juveniles but adults are only found on the reef. Overall, otolith chemistry provides a means of determining the origins and movement of fish, allowing the estimation of contribution rates of the different nursery sites (e.g., Gillanders 2002b; Reis-Santos et al. 2013b). Many studies have demonstrated differences in otolith chemistry among estuarine and coastal habitats (Brown et al. 2019; Russell et al. 2021; Tanner et al. 2012), which is a key precursor for determining connectivity between habitats. To demonstrate connectivity additional steps are required including being able to match adult fish back to estuaries or juvenile habitats within estuaries and coastal areas using classification approaches (Chittaro et al. 2009; Gillanders 2002b; Reis-Santos et al. 2013b; Tanner et al. 2013). Issues may occur with

increasing the number of baseline sampling sites such that sampling sites are often aggregated (Gillanders 2002b). Alternatively, spatially explicit approaches involving continuous assignment where boundaries between sampling sites are not delineated have recently been used on otolith elemental data (Burns et al. 2020). Such an approach building on models of chemical and isotopic variation (i.e., isoscapes) is likely to be particularly beneficial for fisheries and ecosystem-based management, including to identify critical areas for stock replenishment or target areas for conservation (McMahon et al. 2013; Trueman & St John Glew 2019).

In fully marine settings and for highly migratory fish species with ocean-wide or cosmopolitan distribution such as tunas and billfishes, otolith chemistry has also been used to investigate nursery area use and contribution rates as well as adult movements (Artetxe-Arrate et al. 2021; Fraile et al. 2016; Rooker et al. 2008, 2021; Wells et al. 2021). These species regularly cross management boundaries, often migrating large distances to complete their life cycles and some exhibiting homing behaviour that further complicates stock assessment and management efforts (Collette et al. 2011). Since the physicochemical characteristics of the marine environment are rather homogenous compared to inshore areas (e.g., estuaries) the investigated nursery areas in these species are generally farther apart and the analysed otolith chemical composition includes both trace elements and stable isotopes (Artetxe-Arrate et al. 2021; Fraile et al. 2016). Otolith stable isotope $\delta^{18}\text{O}$ values are particularly reliable markers at large spatial scales (cross ocean basin) due to lower temporal variability compared to other tracers (Rooker et al. 2008; Trueman & St John Glew 2019). As above, baseline libraries or models of chemical and isotopic variation of known nursery areas can be used to then assign adults retrospectively to different nursery/natal areas. Moreover, adult movements in these highly migratory species can also be assessed by analysing the chemical composition along the otolith growth axis to provide information over the lifetime of the individuals (Fraile et al. 2016) or by comparing capture location with natal or nursery origin based on otolith core signatures (Artetxe-Arrate et al. 2021; Rooker et al. 2008). Like individual migration pathway reconstruction in freshwater environments (see above), time series analysis approaches, such

as characteristic-based clustering or behavioural change point analysis, are being increasingly applied to otolith chemical transect data allowing movement reconstruction over individual lifetime and providing valuable continuous information on habitat use patterns and larval dispersal trajectories (Sabetian et al. 2021; Shima & Swearer 2016). Ultimately, technological advances will contribute to increased spatio-temporal resolutions in movement reconstructions (Hanson et al. 2010; Sakamoto et al. 2019) but a key next step to consolidate ecosystem-based management is identifying the mechanisms that determine variations in movement behaviour as well as its consequences. Tying movement to other biomarkers in otoliths will empower managers to have a broader perspective on the significance of differential movement for growth performance to evaluate fish responses to environmental variations, as well as its implications on reproductive success, population biomass or trophodynamics (Chung et al. 2019b; GrønkJær et al. 2013; Oxman et al. 2021; Reis-Santos et al. 2021; Sturrock et al. 2015a) (see sections on Environmental stress and Ecophysiology, Food Webs, and Reproduction).

Food webs and species interactions

Changes in fish diet occur as fish grow, and these ontogenetic shifts often present critical bottlenecks for survival and recruitment. Increasingly, fisheries management aims to include dietary information when modelling sustainability and fish population projections. While still not implemented at a large scale, ecosystem-based fisheries management relies on multi-species models that account for species interactions, of which predator–prey relationships are paramount (Eddy et al. 2021; Heymans et al. 2016). Ecosystem models often include mechanisms that account for prey availability, body size of consumers and prey, natural mortality from predation, and the different trophic positions of fishes across their life history stages (Heymans et al. 2016; Pethybridge et al. 2018). Therefore, effective ecosystem-based fisheries management requires comprehensive assessments of trophic interactions and dietary requirements for fish survival and reproduction.

In modern fishes, stable isotope compositions of nitrogen ($\delta^{15}\text{N}$ values) and carbon ($\delta^{13}\text{C}$ values) are

used in conjunction with stomach contents to estimate trophic positions and basal sources of primary production, respectively (Boecklen et al. 2011). $\delta^{15}\text{N}$ values reflect the weighted-average trophic position of the fish's prey, plus a trophic discrimination factor that results from preferential excretion of the light isotope. Fish $\delta^{13}\text{C}$ values can vary significantly within and across ecosystems, such as across estuarine salinity gradients, due to divergent sources of primary production creating isotopic shifts in baseline organic material (Fry 2002; Davias et al. 2014). Isotope analysis of soft tissues, including muscle, eye lenses, and fin clips, form the basis of trophic level analyses in the modern ocean (Boecklen et al. 2011). However, soft tissues quickly degrade and decompose, with few opportunities for measuring $\delta^{15}\text{N}$ values in historical samples. The basis for understanding fish diets is therefore biased toward modern fishes and their recent feeding history. In addition, most soft tissue isotope signatures are time integrated and continuously change to reflect the most recent dietary isotope signatures and lifetime ontogenetic diet shifts are not preserved. Therefore, as methods advance, isotopic research on the organic matrix of otoliths, vertebrae, eye lenses or fish teeth to reconstruct dietary information is gaining momentum, allied to the chronological properties of these archival tissues, that allow ontogenetic shifts in diet histories to be resolved across time (e.g., Bell-Tilcock et al. 2021; Matsubayashi et al. 2020). These qualities make biogenic hard parts of fishes extremely valuable for the broader goals of effective ecosystem-based fisheries management.

Methodological developments

The tools outlined below serve as 'tracers' of dietary signals, and our ability to interpret these signals rests strongly on controlled, laboratory experiments that validate the behaviour of the tracers. Otolith $\delta^{15}\text{N}$ measurements have been limited by the small amount of N in fish otoliths. Nitrogen in otoliths is in the form of proteins, comprising only 0.1–3% by mass (Campana 1999; Dauphin & Dufour 2003; Thomas & Swearer 2019). Until recently, the majority of $\delta^{15}\text{N}$ studies combined multiple otoliths to obtain enough N for elemental-analysis coupled to isotope ratio mass spectrometry (EA-IRMS) (Godiksen et al. 2019; GrønkJær et al. 2013; Sirot et al. 2017; Vandermyde & Whitledge 2008). However, advances

using a persulfate-denitrifier method, allow N isotope measurements from small, individual otoliths (Cheng et al. 2018; Lueders-Dumont et al. 2018, 2020, 2022). For $\delta^{13}\text{C}$ measurements of organics, otoliths are demineralized prior to isotopic analysis, facilitating measurements of organic C without dilution from the inorganic carbonate C that comprises most of the otolith mass (Godiksen et al. 2019; GrønkJær et al. 2013; McMahon et al. 2011a, 2011b; Sirot et al. 2017; Vane et al. 2018a). Otoliths must be demineralized as the mineral fraction is a tracer of other, non-diet related variables (see Ecophysiology section). While the advantage of the persulfate-denitrifier method is the lower mass requirements for N, one of the primary advantages of EA-IRMS methods is that both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ can be measured from the same otoliths. Micromill sampling, allowing for discrete analyses from juvenile and adult life history, is emerging for $\delta^{15}\text{N}$ (Lueders-Dumont et al. 2022; Vane et al. 2018b) and for $\delta^{13}\text{C}$ (Vane et al. 2018a) analyses of the organic matrix, with higher resolution sampling tied to continued improvements in instrument sensitivity. $\delta^{34}\text{S}$ values in otoliths have also emerged as a useful marker in freshwater systems to identify individuals who spent their early lives feeding in different aquatic habitats such as floodplains, rivers, and/or aquaculture facilities (Bell-Tilcock et al. 2021; Johnson et al. 2012; Weber et al. 2002).

Compound-specific isotopic analysis of amino acids (CSIA-AA) in proteins separates isotopic 'baseline' from 'trophic' patterns more clearly than bulk (non-CSIA) $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ analysis (Chikaraishi et al. 2009; McClelland & Montoya 2002). CSIA-AA of muscle tissues is becoming a widely used technique in ecology, providing additional insight into processes at low trophic levels and physiological processing of nutrients (Skinner et al. 2021; Wyatt et al. 2019). Several studies use CSIA-AA analyses of the otolith organic matrix (McMahon et al. 2011a, 2011b; Vane et al. 2018a, 2018b) but to date, CSIA-AA analysis of otolith proteins has only been conducted for large otoliths, as it requires greater amounts of organic N and C than bulk measurements.

For historical reconstruction of food webs using the aforementioned techniques, two additional methodological factors must be considered. First, due to potential diagenetic alteration of organic matter, cleaning methods may be required when analysing $\delta^{15}\text{N}$ of proteins in otolith fossils as trophic archives

(Das et al. 2021; Lueders-Dumont et al. 2018). Second, identifying contemporaneous baseline $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ changes is required for interpreting dietary or food web structural changes, as for modern studies using $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in fish tissues (Boecklen et al. 2011; Post 2002). Increased sensitivity of CSIA-AA methods allowing for analysis of smaller otoliths will be a powerful tool for reconstructing past food webs as baseline and trophic isotopic signals can be measured in the same specimen. Until then, bulk $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ analyses of shell-bound organics of contemporaneous filter-feeding animals known to record isotopic baselines (e.g., coral skeletal material, bivalve shells; Wang et al. 2015; Das et al. 2021), can be compared with isotopic data from otoliths analysed using the methods mentioned above. Matching the spatial and temporal scale of otolith isotopic records with the isotopic baseline is required for interpreting isotopic changes in historical otoliths.

Groundtruthing stable isotope composition of otolith protein to tissues

Muscle tissues have high concentrations of organic N and C, and are the most frequently measured tissue to extract dietary information and food web structure (e.g., Boecklen et al. 2011; Post 2002). In contrast, otoliths have high concentrations of mineral (calcium carbonate), and low concentrations of organics. Studies have only recently begun to measure the isotopic composition of otolith organics, including studies comparing muscle to otolith organic matrix isotope composition. In the few studies to compare signatures, otolith matrix and muscle protein $\delta^{13}\text{C}$ values are similar and highly correlated with one another, including using CSIA-AA (McMahon et al. 2011a, 2011b) and bulk analyses (Godiksen et al. 2019; GrønkJær et al. 2013; Sirot et al. 2017). The same is true for CSIA-AA $\delta^{15}\text{N}$ values (Vane et al. 2018b) and bulk analyses (Cheng et al. 2018; Lueders-Dumont et al. 2020; Vandermyde & Whitley 2008). Cross-species comparisons revealed the potential for species-level differences in the N isotope fractionation in otoliths (e.g., Atlantic cod (*G. morhua*, and others in the Gadidae family). Yet, otolith matrix $\delta^{15}\text{N}$ values were always highly correlated to muscle and dietary values (GrønkJær et al. 2013; Lueders-Dumont et al. 2018, 2020), and inter-specific differences were largely explained by otolith

size and biomineralization (Lueders-Dumont et al. 2020). A smaller number of studies have assessed paired muscle and otolith matrix $\delta^2\text{H}$ values (Whitledge et al. 2006) and $\delta^{34}\text{S}$ values (Bell-Tilcock et al. 2021; Godbout et al. 2010; Weber et al. 2002). Here too, otolith matrix values were similar to muscle values for both $\delta^2\text{H}$ and $\delta^{34}\text{S}$, therefore reflecting the provenance (for $\delta^2\text{H}$) or diet (for $\delta^{34}\text{S}$) of the fish. The findings of the small number of studies explicitly comparing the isotope composition of soft tissue and the otolith organic matrix are encouraging, indicating the otolith macromolecular matrix preserves isotopic histories comparable to tissues such as muscle. Further field and laboratory experimental validations are needed to understand the universality of these trends and whether non-dietary physiological signals are an important factor in otolith organic isotope records.

Controlled laboratory experiments demonstrate stable isotopes of otolith organics are effective tracers of diet (e.g., GrønkJær et al. 2013; Lueders-Dumont et al. 2020, 2022), with dietary tracing ability of otoliths immune to temperature effects (Godiksen et al. 2019). Overall, otolith proteins rapidly incorporate N from diet (Shiao et al. 2018) and in timescales similar to liver, the tissue with the shortest turnover time (Lueders-Dumont et al. 2022). However, life history stage must be considered, especially for young fish, which may have smaller trophic discrimination factors, including for otoliths (Lueders-Dumont et al. 2022).

Historical ecological baselines

$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ measurements of historical otoliths demonstrate the potential for food web data to inform fisheries management. Gulf of Maine Atlantic cod (*G. morhua*) remain commercially important despite the 1990s fishery collapse, with $\delta^{15}\text{N}$ measurements of midden otoliths from fishing outposts showing that seventeenth century cod were nearly one trophic level higher than the largest modern cod from the same region (Lueders-Dumont et al. 2018). Another study, on commercially harvested American silver perch (*Bardiella chrysoura*) in the Gulf of Mexico, also revealed higher trophic levels of historical fish, a shift that was attributed to anthropogenic impacts on prey and habitat availability (Sirot et al. 2017). These studies show that fisheries managers, by measuring only modern conditions, may have insufficient data

for successfully managing and restoring fisheries. Some of the largest ecological changes in structure likely occurred prior to the modern management efforts. Therefore, ecosystem-based fisheries management should strive to include historical food web data to improve their predictions. Together with growth and age information from otoliths and other calcified structures, reconstructing dietary changes in populations and individuals over time may reveal links between complex life history portfolios, differential movement and migration behaviour seen across many different fish species, and changes in food webs.

We are just beginning to apply geochemical tools and other biomarkers to quantify past food webs. Reconstructing ecological baselines in food webs is an especially critical goal now, as we are likely to miss our climate goals at the same time that fish are a vital source of nutrition globally. Overall, examining how past climate changes affected diets of fishes, as well as quantifying the relative impacts of human- and climate-caused changes on food webs is crucial. Trophic level is the basis of food web structure and moreover, is known to be a plastic trait that is sensitive to shifting prey availability, fish behaviour, and fish habitat among other variables. Identifying past ecological conditions will also allow for concrete ecological benchmarks for informing ecosystem-based fisheries management.

Maturity and reproduction

The proportion of mature individuals present in a population and the frequency of reproductive events during a species' lifetime are key parameters used to estimate stock production and manage fishery populations, and are essential for estimating spawning stock biomass, reproductive output, and yearly recruitment (Murawski et al. 2001; Quinn & Deriso 1999). For fish, collecting such data can be challenging. Size-at-age, age of sexual maturity, and reproductive life histories are commonly estimated through seasonal fishery operations, costly survey observations, and/or histological examinations. Such observations, however, provide only a snapshot in time of a population's reproductive capacity and provide no historical perspective for individuals or populations. This limitation is concerning because

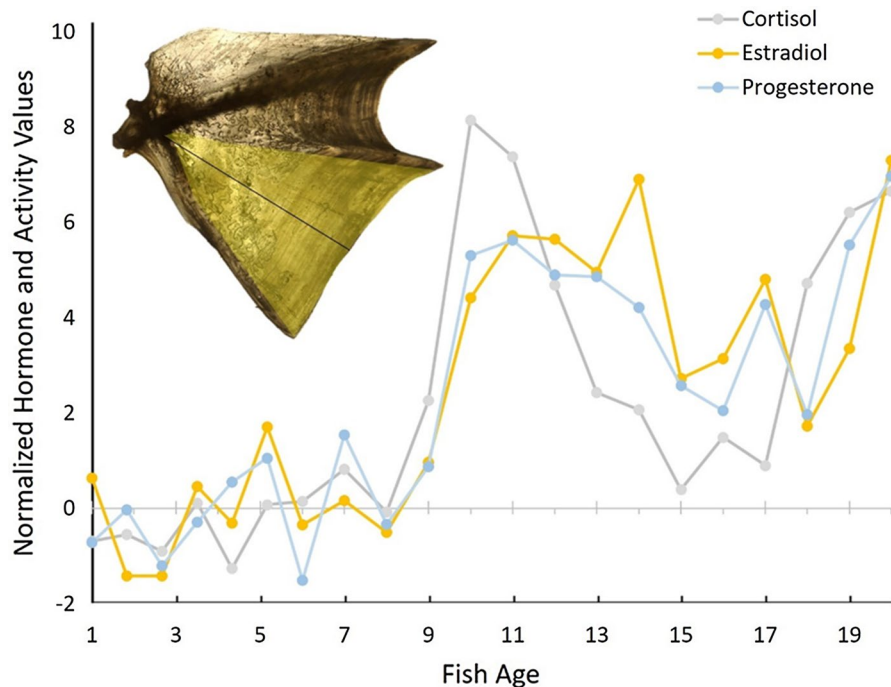


Fig. 3 Cortisol (grey), estradiol (orange) and progesterone (blue) normalized concentrations recovered from annual growth increments within the operculum via immunoassay extraction of a 20-year-old female yelloweye rockfish (*Sebastes ruberrimus*) caught in 2018 (Charapata, Oxman and Trumble, unpublished). The sampled region of the operculum is highlighted yellow (light shade). The entirety of each growth increment was sampled for analysis with the black line showing the trajectory of growth. The currently accepted age of maturity

for yelloweye rockfish is 20 years, but peaks in reproductive hormones (progesterone and estradiol) indicated this individual began to reproduce at 9 – 10 years of age. Cortisol concentrations exceeded those of reproductive hormones between the ages of 9 and 10 but did not appear to have a negative effect. After the onset of maturity, cortisol levels declined significantly until age 18 and there was little evidence of senescence

reproductive stages change seasonally and the relative proportion of individuals estimated within maturity stages can vary depending on the timing of sampling such that estimation of a population's reproductive potential can be biased (Rideout et al. 2005). Also, spawning frequency and senescence, which age-based population models often assume as constant, can vary with age and environment (Rideout & Tomkiewicz 2011). The ability to monitor reproductive reference points over time would improve stock assessments and our understanding of factors influencing reproductive success (Hutchings & Baum 2005).

Fish growth varies seasonally, and these changes are reflected in the structure of incrementally grown archival tissues (e.g., bones and otoliths). Trumble et al. (2013) demonstrated for the first time that in addition to isotopes and elements, reproductive and stress hormones could also be extracted from

incremental growth zones in a baleen whale's ear-plug using a modified Soxhlet method. The resulting age-specific chemical profile was used to estimate the whale's age of sexual maturity, reconstruct its reproductive life history, and assess physiological responses to intrinsic and extrinsic factors throughout its life span. Analysis of cetacean baleen and blubber have yielded similar results (Hunt et al. 2014). Recently, these hormone extraction techniques have been successfully applied to the annual growth increments in bones of several fish species. Charapata et al. (2022) used material removed from the operculae of long lived benthic yelloweye rockfish (*Sebastes ruberrimus*) to reconstruct their reproductive life history (Fig. 3). The opercula of these rockfish have large, well defined annual growth increments from which material is easily sampled. Hormones associated with maturation and reproduction (progesterone,

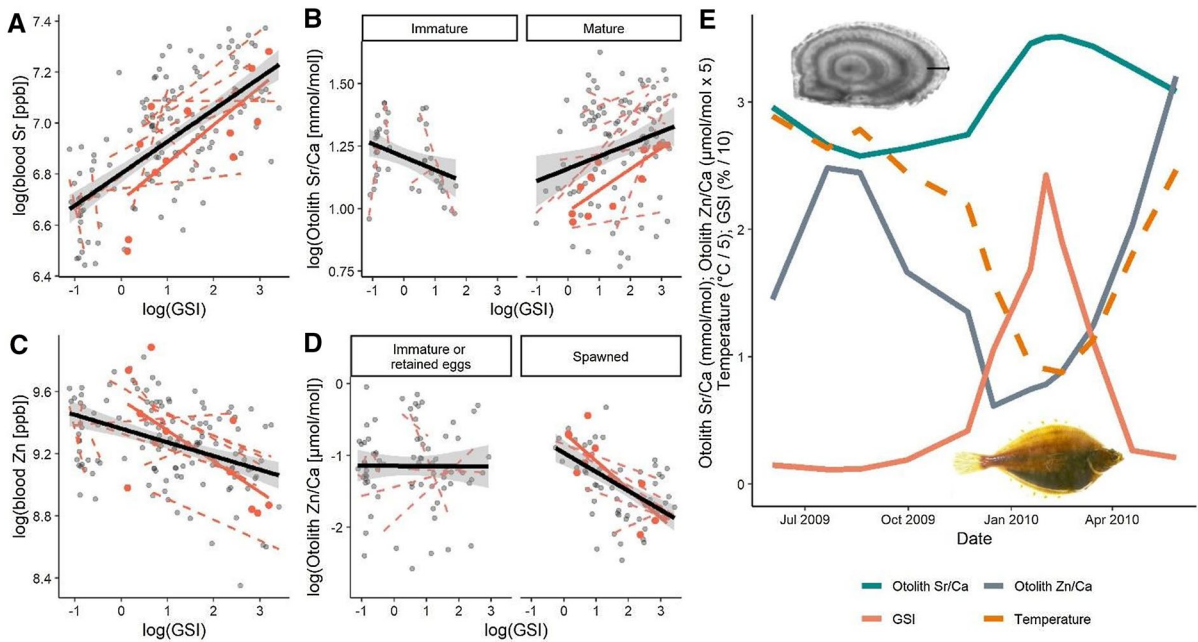


Fig. 4 Potential for reconstructing past spawning events using otolith element concentrations. In tank-reared female plaice (*Pleuronectes platessa*), increased gonadosomatic index (GSI) was associated with increased strontium concentrations in the blood **A** and otoliths of mature females (**B** and **E**), and with reduced zinc concentrations in the blood (**C**) and otoliths of successful spawners (**D** and **E**). A to D show repeat measurements and relationships within individuals (red dashed lines;

fish in **E** highlighted by red circles and solid lines), and the predicted line for the entire population (black line; grey shading showing 95% CI). **E** shows otolith Sr and Zn concentrations, GSI and temperature for one female across the year-long experiment. Inset images show a gravid plaice and a plaice otolith, with the approximate laser track shown as a black line. Data originally published in Sturrock et al. 2014, Sturrock et al. 2015

estradiol) as well as stress (cortisol) were targeted for recovery. Progesterone's role in gamete maturation and reproductive behaviour makes it an ideal indicator of reproductive activity (Pankhurst 2016). Similarly, estradiol is associated with the formation of secondary sexual characteristics, egg development and spermatogenesis. Cortisol is a corticosteroid released in response to stress that can have both inhibitory and stimulatory effects on the endocrine system and behaviour. Although it is not directly involved in reproduction, cortisol is secreted in response to stress and can either enhance or suppress reproduction, depending on the strength of the stress response (Pankhurst 2016). Consequently, cortisol concentrations are often used to assess animal health and environmental disruptions (Chrousos & Gold 1992; Romero et al. 2009). Overall, hormone concentrations varied among annual increments, thereby allowing inferences to be made regarding age of maturity,

reproductive frequency, senescence, and stress levels (Charapata et al. 2022) (Fig. 3).

Lifetime hormone reconstructions have also been conducted with opercula from black rockfish (*Sebastes melanops*) and Chinook salmon (*Oncorhynchus tshawytscha*) as well as vertebrae from bluefin tuna (*Thunnus thynnus*) (Oxman et al. 2021). Opercular bones and vertebra are preferred for this analysis because, relative to otoliths and scales which are typically used to construct biochronologies, their annual growth zones are large and provide the sample mass necessary for hormone extraction.

For management purposes, the ability to construct biochronologies using hormones stored in hard parts provides an effective alternative for assessing a population's reproductive potential relative to more traditional approaches involving costly field surveys or laboratory studies. Moreover, for the first time, it is possible to reconstruct past reproductive activities that can provide insights into drivers of productivity,

trends in abundance, and changes in size and age of maturity. This information could be used to inform forecast and assessment models within the context of environmental change thereby improving the efficacy of management.

While still in its infancy, there is growing interest in the potential for using trace element concentrations in archival tissues such as fish otoliths to reconstruct age at maturity and the frequency of reproductive cycles (Sturrock et al. 2014, 2015a) (Fig. 4, see also Clark et al. (2020), for successful application in mammalian teeth). Given the relative ease and low cost of measuring elemental concentrations at high spatiotemporal resolution across otolith growth rings using LA-ICPMS, and the widespread collection and archiving of otoliths from harvested species, this could provide an economical approach to reconstructing long term shifts in onset at maturity and skipped spawning behaviour to improve the accuracy of metrics such as spawning stock biomass. Because Zn is an important co-factor of collagen proteins, including

otolin-1, and is essential for yolk formation (vitellogenesis), Zn and Ca are the elements most likely to inform these types of analyses due to the elevated concentrations needed for egg production (G. L. Fletcher & King 1978; Hüsey et al. 2021b, Thomas et al. 2019). Pb and Sr are potentially also of interest due to similar behaviours and binding affinities, respectively (Clark et al. 2020; Kalish 1991b; Sturrock et al. 2015a) (Fig. 4). While not easy to measure in otoliths, Se may also be a useful ‘spawning marker’ in the future, being important in vertebrate reproduction (Bedwal & Bahuguna 1994) and showing clear divergence in blood concentrations between mature and immature females and mature male and female fish across the reproductive cycle (Sturrock et al. 2014). The applicability of using element concentrations to reconstruct spawning events is likely to be sex, system and species-specific, and may require multivariate and/or time-series approaches. For example, it was an increase in both concentration and variability in teeth Zn and Pb concentrations that marked the onset of maturity in female walrus (Clark et al. 2020).

As with many previous applications described above, the accuracy of chemical reconstructions will likely be augmented when used in combination with otolith and/or scale microstructural analyses, which often exhibit distinct ‘spawning zones’ relating to ontogenetic shifts in energy allocation (Denechaud et al. 2021; Engelhard & Heino 2005; Irgens et al. 2019). This is a clear area for development in the use of otoliths and calcified tissues and opens a window to go back in time and examine how harvesting and global change have impacted population productivity, maturity and reproductive cycles and to use this information to boost future ecosystem-based fisheries management strategies.

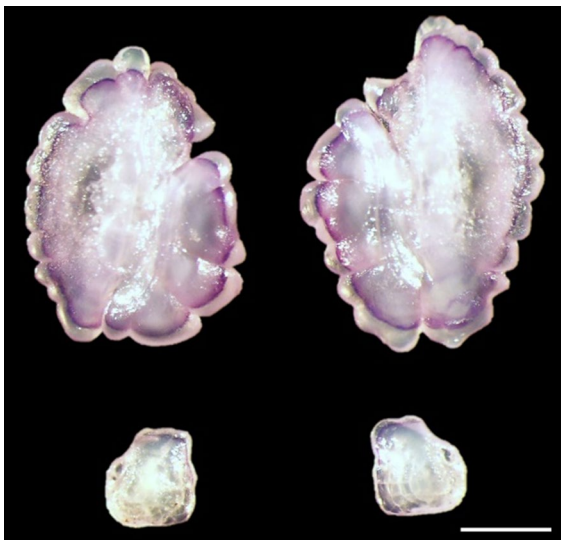


Fig. 5 *Sagittae* (top) and *lapilli* (bottom) otoliths from a reared juvenile snapper (*Chrysophrys auratus*, Sparidae) viewed under a dissecting microscope showing a purple band as a result of marking with alizarin complexone (ALC). The fish (38 mm FL, 60 days old) was immersed in a bath of 10 ppm ALC for 6 h and was sampled six days after staining. Several cohorts of juvenile snapper were marked using this method to differentiate between wild and reared fish as part of a stock enhancement programme in northern Spencer Gulf, South Australia, in 2021 and 2022. The scale bar is 500 μ m (photo – T. Rogers)

Stock enhancement and tracing

Stock enhancement, the practice of rearing fish in a hatchery and releasing them into the wild, is undertaken globally in freshwater, estuarine and marine systems to supplement natural recruitment. This management technique is often implemented where wild populations are heavily depleted or to provide recreational fishing opportunities, and has the potential to enhance other ecosystem functions.

For depleted populations, stock enhancement is used to supplement natural recruitment where the potential for spawning and natural recruitment has been significantly reduced. Similarly, hatchery-reared fish may be stocked into areas where they do not naturally occur to enhance recreational fishing opportunities (e.g., impoundments, reservoirs and dams). Furthermore, it is increasingly becoming a legal requirement for hatcheries in many countries and jurisdictions to enable the identification of escaped fish from aquaculture facilities.

The ability to differentiate between wild and hatchery-reared individuals is fundamental to evaluate the performance of stock enhancement programmes and to quantify the relative contribution of natural and artificial recruitment in wild populations (Curtis et al. 2014; Warren-Myers et al. 2018). Chemical markers provide one option to differentiate between individuals. They can be artificially induced or naturally occurring and are often retained in all calcified structures within a fish (otoliths, scales, bone). Fluorescent compounds such as oxytetracycline, calcein, alizarin complexone, and alizarin red S have been widely used to mark fish for age validation experiments and have also been used for batch marking large numbers of fish for stock enhancement programmes (Fig. 5). Marking of small fish, particularly fingerlings, is best achieved via immersion in a concentrated solution, although the fluorescent compound can also be absorbed from the diet or injection in larger individuals (Crook et al. 2005, 2007; Warren-Myers et al. 2018). Alizarine complexone (ALC) is a fluorescent compound that has been used successfully to mass mark millions of juvenile red sea bream (*Pagrus major*) in Japan since the 1980s (Kitada 2020; Masuda & Tsukamoto 1998). Immersion in ALC has been shown to produce high-quality marks in otoliths and other archival tissues with low mortality rates (i.e., < 5%) and successfully used to quantify the efficacy of restocking (Cottingham et al. 2020; Kitada 2020).

Fish for stock enhancements have also been successfully marked using trace elements (e.g., Sr, rare earth metals) and enriched stable isotopes (e.g., ^{24}Mg , ^{86}Sr , ^{88}Sr , ^{137}Ba , ^{138}Ba). For elements or isotopes to be suitable markers, they must have no effect on the fish, and be simple to apply, long-lasting and non-toxic (Crook et al. 2005; Woodcock et al. 2011). In addition, the cost of the mark, the application

process, and its recovery from marked fish need to be considered for the long-term success of the restocking and monitoring efforts. Although Sr is widely used as an artificial tag, it is naturally occurring across a broad range of concentrations, and so differentiating between artificial and natural signatures can be challenging without a comprehensive understanding of natural variation in water Sr:Ca (Pollard et al. 1999). Subsequently, elements that naturally occur at low concentrations in the environment may provide a more reliable and easier to interpret artificial tag than Sr. Rare earth elements or lanthanides have shown variable success in marking fish especially over short time periods (e.g., Ennevor 1994; Warren-Myers et al. 2018). If either the water or food source differs between wild fish and hatcheries (as well as among hatcheries) then naturally occurring elements may also provide a suitable signature (Johnson et al. 2012; Weber et al. 2002). Similar to Sr:Ca, a comprehensive understanding of natural variation in both the hatchery and the wild is required across a range of spatial and temporal scales. To overcome potential limitations, enriched stable isotopes have been used to unequivocally mark larvae and fingerlings through immersion, dietary spiking, or via the injection of an enriched isotope into the mother (i.e., transgenerational marking). Various enriched isotopes of Ba, Mg and Sr either singly or in combination have been successfully used for marking and identifying hatchery reared fish (e.g., Munro et al. 2008, 2009; Woodcock et al. 2011).

A further method widely used on salmonids, while not a chemical one, involves taking advantage of natural variations in microstructure (Barnett-Johnson et al. 2007) or inducing marks on otoliths through changes in temperature or photoperiod (e.g. thermal marking) (Brothers 1981; Volk et al. 1999; Warren-Myers et al. 2018). Abrupt changes in the physical environment disrupt the daily periodicity of increment formation, which is manifested in the otolith microstructure as a discontinuity in the width and contrast of the daily increment. This approach is more suited towards species that can tolerate abrupt changes in physical conditions.

Numerous otolith marking techniques have demonstrated the capacity to produce distinctive marks in large batches of individuals which are very simple to apply, easily detected, and are suitable for long-term monitoring. However, the most appropriate

technique will depend on the aim of the restocking effort, the number of individuals to be marked, and the availability of funds. For example, fluorescent compounds that retain a distinctive mark for a short period of time are well suited to experimental studies for age validation that consider a small number of individuals. Similarly, batch-marking of large numbers of fish via immersion is a cost-effective technique for long term stock enhancement and monitoring programmes. Combining fluorescent tags, which can be detected non-lethally in the field, with other approaches may also provide a cost-effective approach (Crook et al. 2011). In the end, managers and researchers must consider the characteristics of different compounds and select the most appropriate approach for the objective being undertaken (Crook et al. 2005; Warren-Myers et al. 2018).

Final remarks

Advances in chemical techniques have enabled researchers to tap into information derived from elements, isotopes and biomolecules recorded within the growth layers of otoliths and other incrementally grown tissues, such as eye lenses, vertebrae, operculae and scales. Increasingly, these chemical tracers are being applied for age estimation and to link the impact of differing environmental conditions on the ecology, physiology, and life history expression of fish across habitats and life stages. These emerging technologies combine otolith science with a host of other disciplines, most prominently geochemistry, ecophysiology, metabolism, food provenance and forensics, or trophodynamics, that can be leveraged to support contemporary applications of ecosystem-based fisheries management. While we have summarised several key advances in detecting environmental stressors, other stressors may yet be detectable in the future. We also note some approaches may not yet be necessarily cost-effective for widespread application, however, they already reveal management and conservation-relevant issues, and often already contribute to ongoing monitoring programmes [e.g., Sr isotopes in juvenile and adult otoliths to identify salmon province, nursery habitats, and diversity in outmigration size and timing in California (Cordoleani et al. 2021; Phillis et al. 2018)].

Given the unrivalled time-keeping properties of otoliths, the widespread collection and archiving of otoliths from harvested species provides an economical way to create large reference libraries for connectivity and movement reconstructions (Izzo et al. 2016a). These archives provide links to past ecological conditions from which we can evaluate long-term changes in fish behaviour, physiology and growth performance. Such benchmarks will inform ecosystem-based fisheries management by allowing managers to assess the impacts of stressors such as warming, food web shifts and overfishing on species and population performance. These archives will also allow managers to assess long term changes in age at maturity and skipped spawning behaviour to estimate spawning stock biomass more accurately. Ultimately, coupling multiple lines of evidence extracted from otolith biomarkers (e.g., that trace movement, growth, thermal, metabolic, reproductive, or food web structure) can greatly enhance our ability to manage fisheries more sustainably. Using otolith-derived data to highlight the significance of differential movement for growth performance, evaluate fish responses to environmental variations, as well as implications of those changes for reproductive success, population biomass or trophodynamics will deliver tangible benefits for fisheries managers and the development of ecosystem-based management efforts.

Calcified tissues also provide unequivocal natural tags to test and validate claims on geographical origin, enabling us to confirm whether a product is from where it claims to be, or to assign potential locations of origin for unlabelled products. Overall, there is an underlying need by managers and regulators to understand where aquatic food products originate from, both regarding fishery and aquaculture industries, and for this information to be verifiable. Benefiting from advances in otolith chemistry, reference libraries, and high-throughput methodologies, seafood provenance is a major area for otolith research to advance, catapulting the effectiveness of fisheries and regulatory agencies to combat food fraud (Cusa et al. 2021; Kroetz et al. 2020).

To extract the maximum information from otolith chemical markers, we need a robust and mechanistic understanding of the environmental drivers, physiological regulation and calcification processes that influence otolith development and

composition (Walther 2019). Key research areas include gaining clearer knowledge of the mechanisms governing incorporation of different biomarkers into the proteinaceous and calciferous matrices of the otolith to improve the accuracy of environmental reconstructions (Hüssy et al. 2021b; Thomas et al. 2017; Thomas & Swearer 2019). Improved understanding of the environmental, ecological and phenotypic factors influencing fish responses to stressors, together with continued progress in instrumentation (including, to reduce analytical costs, increase accessibility and sample sizes) will be invaluable to drive the field forward and to increase uptake into routine monitoring and management. Better integrating tissue chemistry approaches with other individual-based measures such as gene expression, genetic markers (Brophy et al. 2020; Reis-Santos et al. 2018a; Tanner et al. 2016), and biologging (Darnaude et al. 2014; Sturrock et al. 2015a; von Leesen et al. 2021) will also help us forecast species responses to pressures such as warming, hypoxia or harvesting. Methodological advances that allow us to take advantage of genetic data archived in otoliths (Momigliano et al. 2019) will also open doorways into long-term changes in fish population structure, gene flow, and effective population size. The analyses of genetic data from otolith collections is an area poised for continued advancement, and offers unique opportunities to identify shifting baselines prior to modern management efforts (Izzo et al. 2016a), and to evaluate long term impacts of environmental stressors and harvesting on genetic diversity. Overall, the goal of using otoliths as biomarkers is to allow us to reconcile management with biological parameters (Kerr et al. 2016), and promote bespoke management actions relevant to specific species, environments, and harvest pressures.

The advances described in this article were made possible by technological breakthroughs, the development of new conceptual frameworks, and through interdisciplinary collaborations. Application of these tools also requires interdisciplinary partnerships and cross-sector knowledge transfer to support sustainable fisheries management. Over the next few years, the true value of these emerging approaches using otoliths and other archival tissues to support fisheries and boost ecosystem-based management will be measured by their successful

implementation into routine monitoring. To ensure widespread uptake and application, the challenge for the research community is to continue to develop, test and demonstrate their benefits, build partnerships with managers and industry, and communicate and translate these innovations widely across academic and applied spheres.

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Author contributions PRS coordinated manuscript preparation, drafted, edited and combined sections. AMS, BMG, BDW, CI, JL-D, KEL, PRS, SET, ZAD, conceptualized the manuscript building on ideas from the WFC 2021 session on biomarkers led by BDW, CI, KEL, PRS, SET. For individual sections, KH, YH, CI, KEL, AHA, DB drafted the section on chemistry to support age estimation; KEL, DB, M-TC, RJ, DSO, CT, BDW drafted the section on environmental stress and ecophysiology; PRS, ZAD, CI, CT drafted the section on seafood provenance; AMS, MW, LJB, JDT drafted the sections on life history diversity in freshwater and diadromous fishes, and linking individual movements with growth; SET, TR, PRS, BMG drafted the section on natal origins and coastal marine nurseries; JL-D and BDW drafted the section on food webs, DSO and AMS drafted the section on maturity and reproduction, with contributions from PC and ST, and TR and BMG drafted the stock enhancement section. All authors contributed and commented on previous versions of the manuscript, read, and approved the final manuscript.

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Declarations

Conflicts of interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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