Environ Biol Fish (2022) 105:327–343
https://doi.org/10.1007/s10641-022-01217-9

Listening with the invasive fish ear: applications and innovations of otolith chemistry analysis in invasive fish biology

Olivier Morissette · Gregory W. Whitledge

Received: 1 June 2021 / Accepted: 10 January 2022 / Published online: 26 January 2022

Abstract Acquisition of biological information on invasive fishes during the early stages of invasion could be critical in orienting subsequent management strategies. To achieve such a task, biological invasion researchers and practitioners take advantage of numerous technologies (e.g. genomics and acoustic telemetry). Surprisingly, the study of invasive fish ecology by analysis of the chemical composition of calcium carbonate hard parts (e.g. otoliths and scales) remains underutilized, despite some convincing examples of successful applications in the scientific literature. Among its most common applications in invasion biology, otolith chemistry has been used to identify natal origins, reconstruct migratory behaviour and assess mixed-stock structure. In this literature review, we provide a general overview of those previous applications but more importantly identify some gaps and obstacles to applications of otolith chemistry in invasion biology and suggest development for innovative applications, including use in wildlife forensic sciences and reconstruction of the early dynamics of invasions.

O. Morissette (✉)
Direction de l'expertise sur la faune aquatique, Ministère des Forêts, de la Faune et des Parcs, Québec City, QC G1S 4X4, Canada
e-mail: olivier.morissette@mffp.gouv.qc.ca

G. Whitledge
Center for Fisheries, Aquaculture and Aquatic Sciences, Southern Illinois University, Carbondale, IL 62901, USA

Keywords Trace element · Stable isotope · Asian carp · Common carp · Sea lamprey · Invasion management · Otolith microchemistry

Introduction

Where do fish go? This question is—in a simplistic manner—fundamental in many fisheries sciences fields, and its answer is crucial for management and conservation. As fishes remain invisible to humans most of the time, scientists have no choice but to rely on instantaneous observations—or snapshots—of fish presence either of high (i.e. acoustic telemetry) or low frequencies (i.e. capture data). For a given region, knowledge of fish occupancies is generally acquired over years to decades, summing various observations (e.g. fish surveys, citizen sightings and museum collections). In invasion biology, however, management actions are generally not conducted with the luxury of time. Thus, information on invasive fish distributions, population structure or natal origins needs to be acquired in a shorter timeframe to be relevant for management (Lodge et al. 2006). Hence, invasive fish biologists have generally been early adopters of many technologies to rapidly assess the fish presence or to inform population control, like electrofishing, which served for the control of common carp (*Cyprinus carpio*) and gars (Lepisosteidae)—the latter being wrongly seen as a pest species—at the end of the 1920s (Burr 1931). Acoustic telemetry has provided the opportunity to track tagged, gregarious species to facilitate the removal of aggregated fish (Judas fish; Bajer et al. 2011; Harris et al. 2020), and, more recently, detection of environmental DNA (eDNA) has opened the way to extensive and rapid detection programs (Jerde et al. 2011). Of the numerous growing technologies, however, the use of fish hard part (e.g. otolith, vertebrae or scale) chemistry appears to not have been adopted as widely in invasive fish management (Carlson et al. 2017).

Of the many structures (e.g. scales, vertebrae, fin rays or otoliths) usable for fish hard part chemistry, otoliths remain the most frequently used. Otoliths are three pairs of structures located in the inner ear of teleost fishes, used for fish hearing and balance. They are primarily composed of a calcium carbonate matrix and a small amount of organic matter, including the protein otolin-1, acting as a template for calcification (Murayama et al. 2002). In addition to calcium, many elements are deposited in minor (> 100 ppm) or trace (< 100 ppm) amounts in otoliths (Campana 1999). This deposition follows a daily regime, controlled by circadian rhythm, that is related in magnitude to somatic growth (Pannella 1971). Concentrations of some trace elements are influenced either by intrinsic (e.g. physiology, growth, reproductive status) or extrinsic factors (e.g. ambient water concentrations, temperature, salinity) at the time of deposition (Campana 1999; Hüssy et al. 2020). Notably, strontium (Sr) and barium (Ba) are shown to be the trace elements, given their kinetic dynamics of deposition in otolith calcium carbonate, to be the most representative of ambient concentrations, representing time-stamped natural tags within otoliths (Hüssy et al. 2020). In marine and estuarine habitats, both elements are efficient proxies for diadromous migration, linked to their differential concentrations between freshwater and saltwater (Elsdon and Gillanders 2005; Walther and Thorrold 2006). In freshwater habitats, strontium variation is mostly linked to bedrock composition and some anthropogenic sources (Walther 2019). Additionally, otolith manganese (Mn) concentration was suggested to be affected by ambient concentrations, although ontogeny, growth rate and exposure to hypoxic waters have been shown to influence concentrations in otoliths (Limburg et al. 2015; Hüssy et al. 2020). Other markers, either trace elements or stable isotopes ratios, are also routinely used to infer biological information from various fish populations. Some examples include otolith oxygen stable isotopes ratios ($\delta^{18}O$), which provide a reliable proxy of past ambient water temperature experienced by fish (Patterson 1998; Darnaude et al. 2014; Morissette et al. 2020) or act as environmental tracers (Norman and Whitledge 2015). Additionally, otolith strontium stable isotopes $^{87}Sr/^{86}Sr$ (Brennan et al. 2019), deuterium $\delta^{2}H$ (Whitledge et al. 2007) and carbon stable isotopes $\delta^{13}C$ (Rude et al. 2017) have also been used as environmental tracers for fish movement and origins.

Such properties have contributed to the application of otolith chemistry in the determination of fish natal origin (Schaeffer et al. 2014; Lazartigues et al. 2016; Maguffee et al. 2019), migratory behaviour (Secor et al. 1995; Elsdon and Gillanders 2003a; Morissette et al. 2016) and population structure (Tanner et al. 2016; Spurgeon et al. 2018; Wright et al. 2018). We consider that such applications could be helpful in invasion biology but remain to be widely adopted. The objective of this literature review is to present the current uses of otolith chemistry in the management of invasive or illegally stocked fish populations. Specifically, we wanted to highlight perceived advantages over other more "traditional" approaches but also identify case studies exemplifying actual applications. We also identified potential gaps and underused applications that could represent the future and innovation leading to a larger contribution of otolith chemistry to the field of invasive fish biology.

Literature review

The systematic review was realized by a search query built of four elements: (1) terms linked to invasive, alien or introduced species, (2) terms linked to otoliths or other fish hard parts (e.g. scales and vertebrae), (3) terms linked to chemistry or stable isotopes and (4) terms linked to invasion dynamics (colonization and dispersion). We included peer-reviewed documents including articles, reports or thesis, both in English and French, resulting from this search query "(alien* OR non-native* OR introduced OR invasive* OR non-indigenous) AND (otolith* or scale* OR vertebra*) AND (chem* OR microchem* OR micro-chem* OR isotope* OR trace element*) AND (origin OR dispers* OR colonis* OR source)" conducted using Web of Sciences, Google Scholar, Google and BioOne search engines. Variations of this query were also tested to retrieve more records. We searched for and included records of the documents published in the period between January 1967 and September 2021. After removal of duplicates, all unique records were evaluated based on a thorough read of the title and abstract and were excluded if not meeting all three predetermined criteria: (1) one of the experimental approaches of the study involve measuring the chemistry (either trace element or stable isotopes) of any fish hard part; (2) one of the study species is considered invasive, non-native or introduced in the studied locality; and (3) the study aimed to directly manage, refine or inform (e.g. risk assessment) management of the studied species. Retained articles' full text was searched for supplementary records by examination of reference lists and citing articles ("cited by" section of publisher website and/or Google Scholar records).

Of the 1908 records analysed, 22 studies were included based on the inclusion criteria, and 6 studies were added after the first round of revision by additional search and reviewer recommendations, including four studies that were published after the initial search (December 2020). Nearly all reviewed documents were scientific journal articles, except one technical report (Macdonald et al. 2010, Table 1). Studies were conducted in the USA (67%, $n=18$), Australia (14.8%, $n=4$), Canada (11.1% $n=3$), New Zealand, Japan and Chile (3.7% each, $n=3$). Specifically, most American studies were located either in the Laurentian Great Lakes or Mississippi River watersheds. Given studied localities, most of the published applications of otolith chemistry in invasion management were conducted in freshwater, with only a handful of studies conducted in estuarine habitats (Thibault et al. 2010; Honda et al. 2012; Araya et al. 2014; Roloson et al. 2020). Applications of otolith chemistry to invasive fishes in marine systems were not encountered in the literature search, which is not the case in the broader applications of otolith chemistry, where estuarine and marine habitats are estimated to represent 56.4% of published management-oriented applications of otolith chemistry (Carlson et al. 2017). Marine habitats are also the most frequently represented in the broader otolith chemistry literature, beyond management-oriented applications (Secor and Rooker 2000; Tanner et al. 2013), and otolith chemistry has a longer history of use in marine fishes compared to the freshwater habitats (Kalish 1989).

Species that were the subject of published otolith chemistry studies were primarily large freshwater cyprinids: common carp (22.2%, $n=6$), grass carp (*Ctenopharyngodon idella*, 7.1%, $n=2$), silver carp (*Hypophthalmichthys molitrix*) and bighead carp (*H. nobilis*, 17.9%, $n=5$). Other studied taxa included salmonids (21.4%, $n=6$) or a mixed group of diverse taxa (14.3%, $n=4$) including some centrarchids. This result is consistent with the geographic distribution of otolith chemistry studies, as common carp, grass carp and bigheaded carps represent species of concern to the Mississippi River, Laurentian Great Lakes and Australia. Three studies were conducted on sea lamprey (*Petromyzon marinus*, 10.7%), some showing promising results of the use of statolith chemistry as a tool for the assessment of origin and migration of jawless fishes (Hand et al. 2008), although some results showed that challenges remain in the interpretation of chemical signals in lampreys' statoliths (see below), especially linked to apparent ontogenetic changes in trace element deposition rate at the adult life stage (Brothers and Thresher 2004; Howe et al. 2013; Dawson et al. 2020).

The main objective of each article was classified into three groups: assessment of migration history, estimation of natal origins and mixed stock analysis. We recognize that those main objectives are sometimes combined with other approaches (e.g. estimation of natal origin to inform study of migration), but the low number of reviewed articles precluded the use of intermediate groups. Of the three objectives, the most common use of otolith chemistry was the identification of natal origins (71.4%, $n=20$). Assessment of the natal origin was used to (in decreasing order) determine the number and identity of potential natal sources (Love et al. 2019; Whitledge et al. 2019), to identify reproduction hotspots (Macdonald et al. 2010; Wolff et al. 2012; Crook et al. 2013) or to identify the most likely source populations of illegal stocking (Wolff et al. 2012; Bourret and Clancy 2018; Love et al. 2019). Otolith chemistry has been used to assess migration behaviour of invasive fishes (21,4%, $n=6$), mainly to determine the frequency of movement between habitats—such as between main channel and wetlands—(Araya et al. 2014; Rude et al. 2017), the invader population expansion strategy (Limburg and Siegel 2006; Thibault et al. 2010) or the seasonal or lifetime migratory behaviour of an invasive fish (Roloson et al. 2020; Morissette et al.

Table 1 Summary of literature review of applications of otolith (and statolith) chemistry by articles, showing species, country, markers used, whether water samples were collected and if the study has a management focus

Objectives	Author	Species	Country	Markers	Water sample?	Management application?
Natal origins	Anderson et al. (2021)	Bigheaded carps	USA	Sr:Ca, Ba:Ca, $\delta^{18}O$	Yes	Yes
	Blair and Hicks (2012)	Koi carp	New Zealand	Ba:Ca, Mn:Ca, Rb:Ca, Sr:Ca	Yes	Yes
	Bourret and Clancy (2018)	Walleye	USA	Sr:Ca, $^{87}Sr/^{86}Sr$	No	Yes
	Brothers and Thresher (2004)	Sea lamprey	USA	Sr, Rb	No	No
	Chapman et al. (2013)	Grass carp	USA	Sr:Ca	Yes	Yes
	Crook and Gillanders (2006)	Common carp	Australia	Ba, Mn, Sr	No	Yes
	Crook et al. (2013)	Common carp	Australia	Ba:Ca, Mg:Ca, Mn:Ca, Sr:Ca, $^{87}Sr/^{86}Sr$	Yes	Yes
	Love et al. (2019)	Bigheaded carps	USA	Sr:Ca, $\delta^{18}O$	No	Yes
	MacDonald et al. (2010)	Common carp	Australia	Ba:Ca, Mg:Ca, Mn:Ca, Sr:Ca, $^{87}Sr/^{86}Sr$	Yes	Yes
	MacDonald and Crook (2014)	Common carp	Australia	Ba:Ca, Mg:Ca, Mn:Ca, Sr:Ca	No	Yes
	Morissette et al. (2021)	Tench	Canada	Ba:Ca, Mg:Ca, Mn:Ca, Sr:Ca	No	Yes
	Munro et al. (2005)	Lake trout	USA	Sr:Ca	Yes	Yes
	Norman and Whitledge (2015)	Bigheaded carps	USA	Sr:Ca, $\delta^{18}O$	Yes	Yes
	Stewart et al. (2021)	Lake trout	USA	Sr:Ca, $^{87}Sr/^{86}Sr$	Yes	No
	Swanson et al. (2020)	Common carp	USA	Al, Ba, Cu, Fe, K, Li, Na, P, Sr	Yes	No
	Whitledge et al. (2007)	Centrarchidae	USA	Sr:Ca, $\delta^{2}H$	Yes	Yes
	Whitledge et al. (2019)	Bigheaded carps	USA	Sr:Ca, Ba:Ca, $\delta^{18}O$	Yes	Yes
	Whitledge et al. (2021)	Grass carp	USA	Ba:Ca, Mg:Ca, Sr:Ca, $\delta^{18}O$, $\delta^{13}C$	Yes	Yes
	Williams et al. (2021)	Bigheaded carps	USA	Sr:Ca, Ba:Ca, $\delta^{18}O$	Yes	Yes
	Wolff et al. (2012)	Non-native piscivores	USA	$^{87}Sr/^{86}Sr$	Yes	Yes
Migration	Araya et al. (2014)	Chinook salmon	Chile	Sr:Ca	No	Yes
	Honda et al. (2012)	Brown trout	Japan	Sr:Ca	No	Yes
	Limburg and Siegel (2006)	Blueback herring	USA	Ba:Ca, Mn:Ca, Sr:Ca	Yes	Yes
	Roloson et al. (2020)	Rainbow trout	Canada	Ba:Ca, Sr:Ca	No	No
	Rude et al. (2017)	VHS-susceptible fish	USA	$\delta^{13}C$	No	No
	Thibault et al. (2010)	Rainbow trout	Canada	Sr:Ca	No	Yes
Mixed-stock analysis	Hand et al. (2008)	Sea lamprey	USA	Ba, Mg, Mn, Pb, Rb, Sr, Zn	No	Yes
	Howe et al. (2013)	Sea lamprey	USA	Ba, Mg, Mn, Sr, Rb, Zn	No	Yes

2021). Identification of mixed-stock composition was the least frequent application (7.1%, $n=2$), which could be a consequence of the relatively rare requirement of such information in invasion biology or lack of applications in the near past.

Most studies were conducted using trace element concentrations from the otolith (53.5%, $n=15$) or in combination with stable isotopes (35.7%, $n=10$). Applications with quantification of stable isotope ratios alone were not frequent (10.7%, $n=3$). Additionally, 53.5% of the published studies were conducted in conjunction with the estimation of water trace element concentrations or stable isotope ratios from the studied region, which is also in contrast with experimental design in marine and estuarine habitats where the most prominent elemental gradient (i.e. salinity) could be assumed to vary positively (Sr) or negatively (Ba), following linear or non-linear relationships, with dissolved Sr or Ba concentrations (Secor and Rooker 2000).

By reviewing those different works, we identified nine broad applications of fish hard part chemistry currently used by managers and researchers at the different stages of the invasion (Fig. 1). Those applications are targeting different otolith regions depending on the study objective, where the otolith core represents the maternal or natal chemical signature, the margin is linked to the chemical signature of the ambient environment at capture and transects provide a lifelong time series of the chemical concentrations from hatching to death.

Case studies

Invasive carps in the Great Lakes basin and origin assessment

The four invasive carps (silver carp, bighead carp, grass carp and black carp (*Mylopharyngodon piceus*)) represent a threat of high concern for the Laurentian Great Lakes. Since their importation in the 1970s, the four species were widely distributed (inadvertently or not) among different watersheds in the USA for biocontrol and weed management, resulting in a slow but steady northern dispersal along the Mississippi River, toward the Laurentian Great Lakes (Kelly et al. 2011). Since the beginning of the 2000s, surveillance and control actions were deployed in the vicinity of the Great Lakes, notably by eDNA surveillance (Jerde et al. 2011), construction of electric barriers (Holliman 2011) and government-funded removal by commercial fishermen. In 2012, four grass carp (LT ranging from 451 to 514 mm) were captured in the Sandusky River, a tributary of Lake Erie. Additional to age determination and ploidy status—which is a proxy of aquaculture origin as many states only allow triploid individuals to be sold (Zajicek et al. 2011; Kinter et al. 2018)—otolith Sr:Ca from those four specimens were compared to otolith Sr:Ca of cultured grass carp sourced in Missouri and Arkansas culture ponds, along with respective water samples (e.g. Sandusky River, Missouri pond and Arkansas pond). Results showed that those diploid (likely of wild origins) specimens had otolith Sr:Ca similar to expected values from the Sandusky River, where high (0.5 to 6 mg/L) strontium concentrations are observed throughout the year, due to the strontium-rich celestite ($SrSO_4$) dolostone bedrocks of its watershed. Altogether, those results pointed toward the capture of four grass carp born in the Sandusky River, providing the first evidence of grass carp recruitment in the Great Lakes Basin (see Whitledge et al. 2021).

Although pinpointing the exact region or habitat where either invader origin or reproduction occurs could be enlightening for management, those applications are only possible later in the invasion process. This is mostly due to the requirement of a minimal number of specimens to provide enough data for building the a priori knowledge of chemical variations for classification (Hand et al. 2008; Crook et al. 2013; Whitledge et al. 2019). Such a priori knowledge can either be in the form of chemoscape, isoscape or intrapopulation variation; however, this is not always a prerequisite for otolith chemistry analysis. Applications without such information—that we will name *without* a priori knowledge approaches—are likely to lead to valuable conclusions if applied in earlier stages of invasion. In the case of the Sandusky River's grass carp, luckily the captured fish recruited and lived in a location with unusually high Sr:Ca for a freshwater system, easing the identification of likely origins of the captured fish. In the absence of such steep elemental gradients, comparison of otolith core material could however inform of the potential presence of single or multiple sources, but actual locations may be difficult or impossible to identify

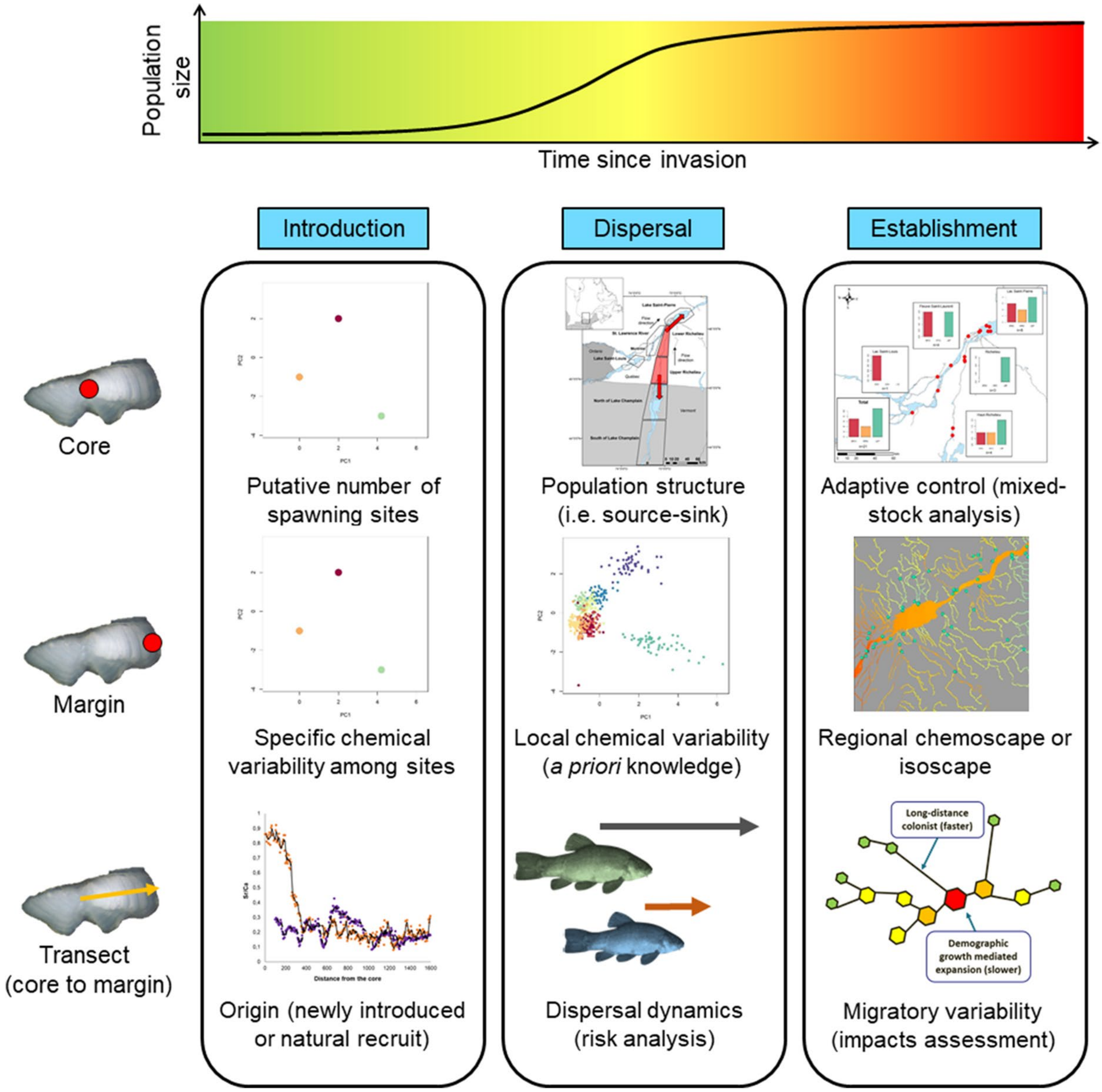

Fig. 1 Summary of common applications of otolith chemistry for management of invasive fishes identified in the current review illustrated in function of the type of data acquired on the otoliths (lines) and invasion stage (columns). Figures and images are original content or reused from Morissette and Sirois (2020) and Morissette et al. (2021). Tench illustrations are modified from the work of Louis L'Hérault (used with permission), and otolith images were taken by one of the authors. Maps of chemoscape were produced in ArcMap 10.4.1 software (ESRI) from unpublished data (Morissette, O)

without additional information on potential sources and their chemical compositions. Admittedly, similar applications are also possible by the use of genetics; however, as early-stage invaders are generally from a single or few introduction events, the population structure could be too low to be detected. Increased access to high-throughput and whole-genome sequencing could, however, provide the possibility to detect very low population differentiation (North et al. 2021) and overcome this limitation. Hence, otolith core chemistry could be highly informative in the early stages of invasion, at least to clarify the existence of single or multiple sources of captured specimens.

Otolith chemistry has been shown to provide sufficient evidence to foresee ecological phenomena before their confirmation with "traditional" approaches. Examples include the suggestion of unknown spawning sites before their formal identification (Morissette et al. 2016) or the existence of previously unknown anadromy (Thibault et al. 2010; Roloson et al. 2020). Comparison of chemical composition along otolith trace element transects could also inform on the homogeneity (i.e. similar migratory pattern) or divergence (i.e. multiple migratory patterns) of an invasive fish life history in a recently invaded system. Such information could efficiently guide eventual detection or monitoring efforts. The potential for an unauthorized fish introduction could be identified by the presence of drastic variation in otolith elemental or isotopic composition along a laser transect (Wolff et al. 2012). One of the major strengths of this approach is the possibility to acquire information early in the invasion process when access to specimens or resources is limiting, as only a handful of specimens are needed to conduct those suggested comparisons. The limitation of such an approach remains that observed variations could be attributable to factors other than environmental influence. Hence, practitioners should proceed with caution when conducting analyses not grounded in known chemical landscapes or with appropriate baselines.

Common carp management in Australia and classification performance

Common carp is a highly successful invader worldwide, cultured and transported by humans for at least 8000 years (Nakajima et al. 2019). In Australia, common carp is considered a major threat, especially in the Murray-Darling basin where, since its establishment in 1962, the population grew to represent around 92% of the common carp biomass of the country (Stuart et al. 2021). Hence, Murray-Darling's carp was the subject of dedicated research and management efforts, mostly to inform its population dynamics and adapt control actions. Among the numerous options explored, otolith chemistry was used to assess recruitment and population structure. Crook and Gillanders (2006) successfully assessed common carp recruitment sources of a single cohort from three lakes of the Barmah-Millewa Forest (BMF) floodplain. Their results showed that 98% of the carp captured downstream of BMF were originating from Barmah Lake and Moira Lake. Therein, they also suggested that potential inter-annual variation in carp otolith chemistry could represent a potential hindrance to future applications. Subsequently, the existence of inter-annual variability in chemical signatures associated with specific nursery grounds was identified, showing that precise determination of production hotspots—either based on capture sites or habitat types—was plausible following the formulation of an annual baseline database of location-specific chemical signatures (Macdonald et al. 2010; Crook et al. 2013). Ultimately, Macdonald and Crook (2014) demonstrated that the use of an annual baseline database provided a significant improvement of classification power of post-larvae origin to their nurseries (53 to 70% of correct classification). Admittedly, the classification procedure was not without error but could provide data sufficiently precise for management applications (e.g. planning of control actions).

The case of Australia's common carp underlines the importance of establishing an adequate baseline for classification to successfully implement otolith chemistry as a management tool for invasive fishes. For cause, one of the many grounds for improvement in applications of otolith chemistry to invasion biology, uncertainties around the classification of chemical composition are the most frequently mentioned. Factors contributing to those uncertainties are numerous, from overlapping water chemical compositions between two or more water bodies (Norman and Whitledge 2015) to poor performance of classification statistical procedures (Blair and Hicks 2012; Swanson et al. 2020). The limitations of the classification procedures are likely to be experienced in applications of otolith chemistry from all study and management fields (including non-invasive fish). That such limitations may be more strongly felt in invasion biology could be potentially linked to the existence of a larger number of putative sources—in case of new invasions that could be sourced from overseas origin—or the environmental and economic consequences at stake. As new invaders could have been introduced from many possible distant habitats—from neighbouring watersheds to another continent—it is inherently more difficult to precisely identify source locations or to obtain new or prior data about the chemistry of all potential source locations. This limitation will not be as important for established invaders (sensu Kocovsky et al. 2018), for which potential sources may be identified and sampled to cover most chemical variability, as demonstrated in Murray-Darling common carp populations (Macdonald and Crook 2014).

Poorly controlled uncertainties could have important management implications, notably by risking inefficient or wasteful management actions if monitoring or control is directed to a water body or a region whose contribution—either as a production hotspot or occupied habitat—has been misidentified (Dana et al. 2019). Classification error could also lead to under- or over-estimating risk posed by an invader based on inferences regarding its ecology (e.g. migration capacity, Morissette et al. 2021) or inconclusive findings in the case of applications in wildlife forensics (Bourret and Clancy 2018).

The establishment of a proper baseline could be produced by the assessment of the natural variation of otolith chemistry among putative sources by the sampling of specimens from the region of interest (which could be part of the control program), when possible (ex. established populations). Otherwise, geography-based approaches could also be implemented; recent developments around the use of interpolated geographical information of water stable isotope ratios (i.e. isoscape) or dissolved trace metals (i.e. metalscape or chemoscape) for identification of source origin, growth habitat or stock structure could be considered for assessment of the origin of invasive fish. Such applications were mostly conducted using strontium stable isotope ratios (Brennan and Schindler 2017; Brennan et al. 2019) or salinity-inferred Sr concentrations (Albertsen et al. 2021). However, the increasing availability of regionalized and high-resolution isoscapes and chemoscape (Bataille et al. 2020) could most certainly be a catalyst of the increased applications of landscape approaches for analyses of otolith chemistry data. Taking advantage of information already acquired by other studies could also help to delineate the chemical portrait of some regions (Hand et al. 2008; Morissette and Sirois 2020; Vu et al. 2021). Such development could represent a significant step forward for application in invasion biology, by improving classification accuracy, allowing for more precise geographical identification of crucial habitats (Chapman et al. 2013), increasing the coverage of more chemical signatures from putative sources habitats (Howe et al. 2013) and inclusion of a more realistic control of uncertainties.

For the common carp invasion in Australia, otolith chemistry ultimately contributed to clarifying the population structure (Crook and Gillanders 2006; Macdonald et al. 2010; Crook et al. 2013; Rahel and Smith 2018). Macdonald and Crook (2014) also provided a framework to apply post-larvae nurseries' origin in the assessment of hydrology's influence on cohort strength. Such innovations had a real potential to serve in water management in the Murray-Darling system, to promote control (or decrease of opportunity) of common carp or even conservation of other native species, by promoting suitable conditions for spawning and recruitment. Ultimately, the recruitment survey by otolith chemistry was not included—at the time of writing this review—in Australia's National Carp Control Plan (NCCP, https://carp.gov.au). Though yet to be applied in a management context, this is not related to the performance of the technique. Rather, it is more a consequence of the ephemeral nature of academic research, where short funding cycles make it more difficult to translate research findings into management outcomes (Jed Macdonald, *pers. comm.*).

Guidance of sea lamprey control and considerations on biomineralization

Since the invasion of the Great Lakes by the sea lamprey (*Petromyzon marinus*) and the consequent dramatic decline of many commercial fisheries, extensive resources have been invested into the development and application of control methods. The use of lampricide (3-trifluoromethyl-4-nitrophenol, TFM) remains the most efficient tool to keep sea lamprey populations in check. TFM treatments are targeted to streams based on numerous factors, including time since last treatment, larvae density and size structure, the proportion of larvae likely to undergo metamorphosis and cost (Christie et al. 2003; Fenichel and Hansen 2010). Larval density, however, is an imperfect proxy for effort allocation as it remains to be confirmed as a robust predictor of parasitic adult abundance and returning spawners; evidence suggests that the relationship is not straightforward and could be context-dependent (Jones 2007). Ultimately, adaptive management—based on estimation of the stream's contributions to the Great Lakes populations—could drastically improve the efficiency of the program. The peculiar life cycle of the sea lamprey, which consists mostly of filter-feeding ammocoetes buried in stream sediments, precludes the use of several techniques of mixed-stock assessment and spawning contribution (e.g. capture-mark-recapture, genetics).

To overcome technical limitations, the use of statolith chemistry—the analog structure to otoliths in lampreys—was suggested to be a promising tool in the estimation of larvae-to-adult metamorphosis survival and spawner's contributions to populations. The results of Brothers and Thresher (2004) were promising, showing 90% correct classification of ammocoetes captured in St. Marys River (connecting Lake Superior and Lake Huron) and Lake Huron streams, suggesting that the approach could be applied to mixed-stock assessment. These results were replicated by Hand et al. (2008), who achieved an overall 83% of correct classification of ammocoetes captured in 13 streams from the Great Lakes (e.g. Lakes Huron, Michigan and Superior). Those results show how classification could greatly vary in performance among water bodies and systems, even for the same species, and expose how classification accuracies remain a critical aspect of otolith and statolith chemistry for the management of invasive fishes. The reliance on multi-parameter classification in those studies (achieved with 5 to 7 elements) showed that stream-based classification was feasible.

Admittedly, improvement of the inference made by the analysis of otolith composition and its applications (i.e. source identification, migration reconstruction and mixed-stock analysis) is not a goal unique to the management of invasive species. This subject has been vastly covered in different works (Mercier et al. 2010; Jones et al. 2016), concluding that the strategy for improvements of classification lies notably in increasing the numbers of elemental markers and improvement of classification statistical procedures. Whereas this fact is not representing a problem when analyses are conducted with diadromous fishes (Thibault et al. 2010; Roloson et al. 2020), achieving sufficient classification accuracy in freshwater habitats may be more challenging based on few chemical markers or when conducted in a less predictable chemical landscape (Pracheil et al. 2014). Multivariate analyses of otolith composition have shown the potential for sensible improvement of classification even with the sole inclusion of one additional element (Mercier et al. 2012; Morissette and Sirois 2020) or the use of performant classification procedures based on boosted regression trees (Mercier et al. 2010) or machine learning (Random Forests, Breiman 2001). We recognize, however, that inclusion of additional elements, without a clear understanding of the biomineralization process, could be misleading if observed variations are not linked to an environmental factor (Jones et al. 2016).

Adult sea lamprey reclassification by Howe et al. (2013) in Lake Champlain is an eloquent demonstration of the importance of an in-depth understanding of biogenic carbonates biomineralization. Whereas ammocoetes were successfully reclassified to natal streams with 57.1% correct (70.2% using a clustering approach), adult reclassification success was really poor (3%). This result was worse but concordant with Brothers and Thresher's (2004) 44% success rate for classifying (versus 90% for ammocoetes). Although the annual baseline for classification could have improved classifications of adults, Howe et al. (2013) also proposed a second line of evidence where post-depositional reworking of statoliths between larvae and adult stages may contribute to this decrease of classification accuracy. Examination of statoliths presence and size by Barker et al. (1997) showed a decoupling of statolith size versus ammocoete length in some Great Lakes streams and prevalence of absence of statolith in metamorphosing lampreys, suggesting potential resorption linked to a calcium-limited environment or physiological demands. Without a clear description of this potential phenomenon, the use of statolith chemistry reclassification for the establishment of sea lamprey adaptive management will remain uncertain.

Biomineralization of trace elements in biogenic carbonates is a complex phenomenon, and inferences on environmental history and habitat utilization using elements which deposition is influenced by physiology or temperature (Elsdon and Gillanders 2003b; Sturrock et al. 2015; Izzo et al. 2018) may not represent true spawning origin or migratory behaviour. As understanding of biogenic carbonate mineralization is improving (Hüssy et al. 2020), practitioners will be more able to draw appropriate conclusions based on multivariate otolith composition, and the potential gain in classification accuracy should be envisioned in the future studies. For fish species for which knowledge of the biomineralization process remains to be defined, laboratory-based studies of the process are critical (Wells et al. 2003; Izzo et al. 2018). Such studies should be planned for fish species listed on the different priorities list (e.g. IUCN 100 of the World's Worst Invasive Alien Species or the Great Lake Commission Least Wanted list) for which preliminary knowledge is still not available.

Underused applications

Applications of mixed-stock assessments

This review provided a general view of the potential applications of otolith chemistry in the management of invasive fish (Fig. 1). We are also showing that, among current uses, mixed-stock assessment is a marginal application in the management of invasive fish. It represented only 7.4% of the principal objective of the reviewed studies; however, this application represents up to 36% of studies when considering the 250 (of 1514 screened) management-oriented use of otolith chemistry published between 1967 and 2015 reviewed by Carlson et al. (2017). Mixed-stock analysis, the identification of the natal origin of fish captured in the course of important fisheries activities, is generally intended for monitoring of exploited fish stock to inform and implement sustainable harvest (Secor 2013). As such objectives are not part of invasive fish management, the rarity of this application in invasion biology seems intuitive. However, monitoring of stocks structure, specifically in terms of the origin of harvested individuals or changes in mixed-stock composition before and after implementation of management actions, could be considered in investigations regarding the management of invasive fishes, especially in estimating the efficiency of a control program (Whitledge et al. 2019). Moreover, the identification of the relative contribution of different spawning sites could promote a more adaptive control (Crook et al. 2013; Whitledge et al. 2021), channelling the focus for sampling on the most productive component of the invader's stock or promoting local functional eradication (Green and Grosholz 2021). Such applications could be envisioned in marine systems, where performance of classification by otolith chemistry seems precise enough for adaptive control of marine invaders (e.g. lionfish *Pterois volitans*). Adaptive planning of a control program will have to be based on accurate classification models, for which baseline data (see common carp case study) may be required owing to the local variability of water chemistry or the species of interest. Hence, the mixed-stock analysis represents a strategic second step, or revitalization, if such baseline data have been acquired as part of early assessment of the invasion in the management of expanding invasive fish for which such studies have already been conducted.

Wildlife forensics in invasion management

The use of fish hard parts chemistry in wildlife forensics is a promising innovation in the management of invasion and unauthorized introductions. Notably, variations in chemical composition could help in the identification of introduced fish or document the time since introduction. Based on otolith Sr:Ca values, illegal transplants of lake trout (*Salvelinus namaycush*) in Yellowstone Lake (WY, USA) were described with great precision (Munro et al. 2005). By the comparison of otolith core and margins Sr:Ca from specimens of known Wisconsin's lake trout populations, Munro et al. (2005) described the regional inter-lake variability and the intra-lake stability of the Sr:Ca values. Assessment of otolith core Sr:Ca from Yellowstone Lake trout resulted in the identification of potential transplanted specimens and their most likely source (Lewis Lake). Moreover, the presence of abrupt changes in Sr:Ca along otolith transects (from core to margin) of trout identified as "transplants" allowed for the estimation of the timing of two introduction events (1989 and 1996). Because genetic analyses of origin may be limited in such a scenario, this example demonstrates the fitting complementarity of both approaches in wildlife forensic of illegal transplants. As unauthorized fish introduction may lead to a drastic change in the fish community and represent a significant driver of fish population perturbation (Rahel and Smith 2018), otolith chemistry may represent a well-suited approach in the assessment of this introduction pathway to prevent further introductions. The improvement of a priori knowledge on regional to national chemical variation may also provide otolith chemistry forensics appreciable gain. With the growing trend in the creation and improvement of publicly available isoscapes and metalscapes, routine identification of the most likely sources of illegal introduction should be considered a realistic avenue.

Identification of likely origin of exotic or invasive species based on hard parts chemical composition could also be crucial in deterrence and law enforcement. Notably, the chemical composition of biogenic carbonates has already contributed to a criminal case of illegal harvest and transportation (Wolff et al. 2012). Generally, the use of evidence in criminal cases requires high confidence and extensive validation of the analytical process, to perform analysis under quality assurance standards comparable for wildlife forensics genetics (Ogden et al. 2009). Hence, the rigorous standards required in informing wildlife-related prosecution may not be met in systems where significant overlap among chemical signals exists, causing low classification performance or uncertainties that remain difficult to control. The inclusion of stable isotope markers that exhibit regional to continental-scale stability (e.g. $\delta^{18}O$ or $\delta^{2}H$) or combined use of genetic data could refine classification performance in order to improve standards. In addition to the assessment of potential pathways of introduction or informing criminal cases, otolith chemistry could act as a deterrence tool where citizens are informed that illegal introductions could be traced back to their point of origin. Bourret and Clancy (2018) provided an eloquent example of such utilization, with an accurate model of classification (95% of correct identification) leading to reliable identification of the potential source of walleye illegal introduction.

Finally, the chemical composition of fish hard parts could provide a means of surveillance and monitoring of the organisms-in-trade pathway. For example, stable isotope values and trace element concentration profiles have been successfully used for the assessment of seafood provenance (Gopi et al. 2019; Daryanani et al. 2021) on both local and global scales, enabling for a posteriori verification of seafood shipment and enforcing compliance for source labelling. Such use could be an efficient complementary approach to genetic verification steps used in the aquarium trade, surveillance of shipment (e.g. grass carp sterilization, Zajicek et al. 2011; Kinter et al. 2018) and biocontrol regulation. Hence, conservation and wildlife enforcement agencies could certainly benefit from the integration of fish hard parts chemistry—owing to their capacity to overcome challenges identified—within their investigation branch, especially in regions where a priori knowledge on water chemistry is available.

Innovations and next steps

During this review, we identified applications of otolith chemistry that remain to be used in the realm of invasion biology. For practitioners and researchers from other domains relying on otolith chemistry, those applications may not appear novel per se, but our experience in both invasion biology and otolith chemistry suggests that their contribution may be valuable for the advance of invasion biology. Notably, two avenues seem promising in the diversification of applications; the a posteriori study of invasions dynamics and the application to other biogenic carbonates.

Study of past invasion dynamics using historic otolith samples

Being mostly a mineral structure, otoliths display high chemical stability, which allows for reliable analyses of trace elements and stable isotopes values in historic—even archaeological—samples (Patterson 1998). Avigliano et al. (2020) showed that archaeological otoliths could be used to infer fish behaviour of Late Holocene (1000 ^{14}C yr BP) *Genidens barbus* found on Patagonian hunter-gatherer sites. Identified migratory behaviours were similar to modern specimens, suggesting stability in life-history strategies for the species and clarifying prehistoric human food sources. As otolith and other fish hard parts are routinely sampled and conserved by many management organizations, a real potential exists to access and analyse the historical life history of an invasive fish species during the first moments of an invasion.

For example, analyses of trace element concentration in the otolith cores of first captured specimens of a new invader in a given locality may inform on the number of introduction and/or colonization events that have led to the successful invasion. Moreover, the study of migration behaviour and population structure of invasive fish in their early stage of invasion could provide information on invasion dynamics in a given region but also factors of successful or failed invasions. For example, identification of the elemental signatures of a spawning ground used in the early stages of the invasion, but which then appears abandoned later in the invasion, may suggest a failed attempt by the species. The analysis of the environmental factors linked to the failed attempts could clarify the dynamics of the success of an invasion for this given species, providing new insights on the prediction of invasion success, one of the so-called invasion holy grails (Davis et al. 2000; Catford et al. 2009). Additionally, the study of biomarkers deposited in the otolith matrix could inform on conditions ($\delta^{18}O$ for temperature and $\delta^{15}N$ for trophic status) or physiological conditions (ex. $\delta^{13}C$ for fish metabolism) prevailing during the early stages of invasion and contributing to invasion success.

There are important limitations to this approach, notably the alteration of the chemical composition of historic otolith samples and the long-term chemical stability of studied waterbodies. Even if otoliths are fairly stable to degradation—given their low content of organic material—and heat alteration (Andrus and Crowe 2002), preservation protocols and past treatment in the laboratory (e.g. staining or use of microscope oil) may have altered their chemical composition (Hedges et al. 2004; Storm-Suke et al. 2007). The history of those potential treatments should be determined beforehand. A possibility also exists that human-made structures (e.g. dams, ports), waste production or catastrophic events (e.g. landslides, hurricanes) may have significantly modified contemporary hydrology—which could influence evaporation, isotopic ratios and water-carbonate fractionation (Chamberlayne et al. 2021)—or the concentration of some trace elements (i.e. Sr can be linked to anthropogenic sources) compared to their historic states. As routine analyses of the water trace element concentrations (or stable isotopes ratios) are fairly recent (Morissette and Sirois 2020), chances are such historic information is not available. The source of potential modification of water chemical or isotopic values should be traced back to assure potential stability.

Use of other biogenic carbonates

Finally, some of the identified and presented applications (Fig. 1) could be envisioned for other biogenic carbonates, enabling the applications for other aquatic taxa. Calcium carbonate deposition in mollusc and crustacean shells (e.g. crayfishes, crabs, cephalopods) are plausible applications in invasion biology, as knowledge on trace metal uptake and deposition for those taxa are recently progressing (Rainbow 1997; Dar et al. 2018). Identification of spawning origin and population structure was successfully demonstrated in a South Florida blue crab (*Callinectes sapidus*) population (Williams 2013). Similar developments were made with arthropods like the cotton bollworm (*Helicoverpa armigera*), where chemical composition could inform biosecurity control, a model that could easily be integrated into invasion biology settings (Holder et al. 2014). For example, classification of potential origin from the chemical composition of mollusc shells by large-scale isoscapes could also provide an efficient means of identification of sources of overseas boat or other nautical equipment biofouling (Ricardo et al. 2015) or distribution chains in contaminated goods (e.g. zebra mussel-contaminated Marimo balls). Examples in surveillance of seafood traceability and surveillance of the supply chain by calcium carbonate hard parts are an eloquent demonstration of possible development for prevention or surveillance of biological invasion by fish (and non-fish) (Daryanani et al. 2021). The main limitations in the application of stable isotope or trace element concentrations in the assessment of the origin of invertebrates reside in the uncertainty of the hard part biomineralization process for some of these species and the shorter turnarounds of chemical signals in invertebrates (notably linked to shell moulting), which may decrease the possibility to infer past events or increase the intra-population variability. Post-depositional alteration of chemical composition of other biogenic carbonates may also alter trace element concentrations or stable isotope ratios, a phenomenon that still needs to be better described.

Conclusions

Where do fish go? This was and remains a central question of many aquatic sciences, including invasion biology. This review enabled us to weigh and characterize the use of otolith chemistry in the management of invasive fish. Adoption of this technology remains low in the field, mostly because of the difficult management of classification uncertainties, which could be improved by better classification models (i.e. better experimental design or higher numbers of relevant markers), reliance on geographical approaches (i.e. isoscape or metalscape) or embracing the strength of without a priori knowledge approaches. Most uses in biological invasion study and management were focussed on the identification of spawning origin and migration, with mixed-stock analysis remaining a seldom-used approach. We are suggesting, however, that the latter application could find a valuable place in the management of control actions or wildlife forensics. Fish hard part chemistry analysis and sclerochemistry are growing fields, and expansion in the relative number of published studies in the last decade seems to support this view (Walther 2019). Recent gains in our understanding of biomineralization (Thomas and Swearer 2019; Hüssy et al. 2020) makes us believe that its use will continue to percolate into invasion biology. The future development may tend to reduce uncertainties in data interpretation, but two innovative applications—the use of historical otolith samples for the reconstruction of past invasion dynamics and development of the use of calcified structure chemical composition from other aquatic taxa (i.e. molluscs or crustaceans)—appear fairly promising for research and management of biological invasions and should probably guide the future questions we should ask.

Acknowledgements We are grateful to many colleagues for discussions and thoughts about this work, mainly to the participants of the 2021 CCFFR-SCL conference, where this material was first presented. We also thank Dr. Jed Macdonald and one anonymous reviewer for the revision of this manuscript, which greatly improved the manuscript.

Data Availability Specifics of literature review search queries are provided in the main text.

Declarations

Ethical approval This is a study based on a review of published articles, and no ethical approval is required to conduct the research.

Conflict of interest The authors declare no competing interests.

References

Albertsen CM, Hüssy K, Serre SH, Hansen JH, Thomsen TB (2021) Estimating migration patterns of fish from otolith chemical composition time-series. Can J Fish Aquat Sci. https://doi.org/10.1139/cjfas-2020-0356

Anderson CL, Whitledge GW, Rude NP, Lamer JT (2021) Using otolith chemistry to determine early life environments and movement of the emerging bigheaded carp population in Pools 16–19 of the Upper Mississippi River. N Am J Fish Manag. https://doi.org/10.1002/nafm.10679

Andrus CFT, Crowe DE (2002) Alteration of otolith aragonite: effects of prehistoric cooking methods on otolith chemistry. J Archaeol Sci 29(3):291–299. https://doi.org/10.1006/jasc.2001.0694

Araya M, Niklitschek EJ, Secor DH, Piccoli PM (2014) Partial migration in introduced wild chinook salmon (*Oncorhynchus tshawytscha*) of southern Chile. Estuar Coast Shelf Sci 149:87–95. https://doi.org/10.1016/j.ecss.2014.07.011

Avigliano E et al (2020) Otoliths as indicators for fish behaviour and procurement strategies of hunter-gatherers in North Patagonia. Heliyon 6(3):e03438. https://doi.org/10.1016/j.heliyon.2020.e03438

Bajer PG, Chizinski CJ, Sorensen PW (2011) Using the Judas technique to locate and remove wintertime aggregations of invasive common carp. Fish Manage Ecol 18(6):497–505. https://doi.org/10.1111/j.1365-2400.2011.00805.x

Barker LA, Morrison BJ, Wicks BJ, Beamish FWH (1997) Notes: Age discrimination and statolith diversity in sea lamprey from streams with varying alkalinity. Trans Am Fish Soc 126(6):1021–1026. https://doi.org/10.1577/1548-8659(1997)126%3c1021:NADASD%3e2.3.CO;2

Bataille CP, Crowley BE, Wooller MJ, Bowen GJ (2020) Advances in global bioavailable strontium isoscapes. Palaeogeogr Palaeoclimatol Palaeoecol 555:109849. https://doi.org/10.1016/j.palaeo.2020.109849

Blair JM, Hicks BJ (2012) Otolith microchemistry of koi carp in the Waikato region, New Zealand: a tool for identifying recruitment locations? Inland Waters 2(3):109–118. https://doi.org/10.5268/IW-2.3.480

Bourret SL, Clancy NG (2018) Using forensic geochemistry via fish otoliths to investigate an illegal fish introduction. Can J Fish Aquat Sci 75(11):1778–1783. https://doi.org/10.1139/cjfas-2018-0082

Breiman L (2001) Random Forests. Mach Learn 45(1):5–32. https://doi.org/10.1023/A:1010933404324

Brennan SR, Schindler DE (2017) Linking otolith microchemistry and dendritic isoscapes to map heterogeneous production of fish across river basins. Ecol Appl 27(2):363–377. https://doi.org/10.1002/eap.1474

Brennan SR, Schindler DE, Cline TJ, Walsworth TE, Buck G, Fernandez DP (2019) Shifting habitat mosaics and fish production across river basins. Science 364(6442):783. https://doi.org/10.1126/science.aav4313

Brothers E, Thresher R (2004) Statolith chemical analysis as a means of identifying stream origins of lampreys in Lake Huron. Trans Am Fish Soc 133(5):1107–1116. https://doi.org/10.1577/T03-139.1

Burr JG (1931) Electricity as a means of garfish and carp control. Trans Am Fish Soc 61(1):174–182. https://doi.org/10.1577/1548-8659(1931)61[174:EAAMOG]2.0.CO;2

Campana SE (1999) Chemistry and composition of fish otoliths: pathways, mechanisms and applications. Mar Ecol Prog Ser 188:263–297. https://doi.org/10.3354/meps188263

Carlson AK, Phelps QE, Graeb BDS (2017) Chemistry to conservation: using otoliths to advance recreational and commercial fisheries management. J Fish Biol 90(2):505–527. https://doi.org/10.1111/jfb.13155

Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a

single theoretical framework. Divers Distrib 15(1):22–40. https://doi.org/10.1111/j.1472-4642.2008.00521.x
Chamberlayne BK, Tyler JJ, Gillanders BM (2021) Controls over oxygen isotope fractionation in the waters and bivalves (*Arthritica helmsi*) of an estuarine lagoon system. Geochem Geophys Geosyst 22(6):e2021GC009769. https://doi.org/10.1029/2021GC009769
Chapman DC et al (2013) First evidence of grass carp recruitment in the Great Lakes Basin. J Great Lakes Res 39:547–554. https://doi.org/10.1016/j.jglr.2013.09.019
Christie GC et al (2003) Selecting great lakes streams for lampricide treatment based on larval sea lamprey surveys. J Great Lakes Res 29:152–160. https://doi.org/10.1016/S0380-1330(03)70484-5
Crook DA, Gillanders BM (2006) Use of otolith chemical signatures to estimate carp recruitment sources in the mid-Murray River. Aust River Res Appl 22(8):871–879. https://doi.org/10.1002/rra.941
Crook DA et al (2013) Recruitment sources and dispersal of an invasive fish in a large river system as revealed by otolith chemistry analysis. Can J Fish Aquat Sci 70:1–11. https://doi.org/10.1139/cjfas-2012-0504
Dana ED, García-de-Lomas J, Verloove F, Vilà M (2019) Common deficiencies of actions for managing invasive alien species: a decision-support checklist. NeoBiota 48:97–112
Dar MA, Belal AA, Madkour AG (2018) The differential abilities of some molluscs to accumulate heavy metals within their shells in the Timsah and the Great Bitter lakes, Suez Canal, Egypt. Egypt J Aquat Res 44(4):291–298. https://doi.org/10.1016/j.ejar.2018.11.008
Darnaude AM et al (2014) Listening in on the past: what can otolith δ18O values really tell us about the environmental history of fishes? PLoS ONE 9(10):e108539. https://doi.org/10.1371/journal.pone.0108539
Daryanani DS, Martino JC, Doubleday ZA (2021) Statolith chemistry: a new tool to understand the ecology and provenance of octopus. Rev Fish Biol Fisheries. https://doi.org/10.1007/s11160-021-09671-x
Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88(3):528–534. https://doi.org/10.1046/j.1365-2745.2000.00473.x
Dawson HA, Higgins-Weier CE, Steeves TB, Johnson NS (2020) Estimating age and growth of invasive sea lamprey: a review of approaches and investigation of a new method. J Great Lakes Res. https://doi.org/10.1016/j.jglr.2020.06.002
Elsdon TS, Gillanders BM (2003a) Reconstructing migratory patterns of fish based on environmental influences on otolith chemistry. Rev Fish Biol Fisheries 13(3):217–235. https://doi.org/10.1023/B:RFBF.0000033071.73952.40
Elsdon TS, Gillanders BM (2003b) Relationship between water and otolith elemental concentrations in juvenile black bream *Acanthopagrus butcheri*. Mar Ecol Prog Ser 260:263–272. https://doi.org/10.3354/meps260263
Elsdon TS, Gillanders BM (2005) Strontium incorporation into calcified structures: separating the effects of ambient water concentration and exposure time. Mar Ecol-Prog Ser 285:233–243. https://doi.org/10.3354/meps285233
Fenichel EPFP, Hansen GJAHJA (2010) The opportunity cost of information: an economic framework for understanding the balance between assessment and control in sea lamprey (*Petromyzon marinus*) management. Can J Fish Aquat Sci 67(1):209–216. https://doi.org/10.1139/f09-163
Gopi K, Mazumder D, Sammut J, Saintilan N, Crawford J, Gadd P (2019) Combined use of stable isotope analysis and elemental profiling to determine provenance of black tiger prawns (*Penaeus monodon*). Food Control 95:242–248
Green SJ, Grosholz ED (2021) Functional eradication as a framework for invasive species control. Front Ecol Environ 19(2):98–107. https://doi.org/10.1002/fee.2277
Hand CP, Ludsin SA, Fryer BJ, Marsden JE (2008) Statolith microchemistry as a technique for discriminating among Great Lakes sea lamprey (*Petromyzon marinus*) spawning tributaries. Can J Fish Aquat Sci 65(6):1153–1164. https://doi.org/10.1139/F08-045
Harris C et al (2020) Movement and space use of Grass Carp in the Sandusky River, Ohio: implications for Lake Erie eradication efforts. North Am J Fish Manag 40(2):513–530. https://doi.org/10.1002/nafm.10560
Hedges KJ, Ludsin SA, Fryer BJ (2004) Effects of ethanol preservation on otolith microchemistry. J Fish Biol 64(4):923–937. https://doi.org/10.1111/j.1095-8649.2004.00353.x
Holder PW et al (2014) Isotopes and trace elements as natal origin markers of *Helicoverpa armigera* – an experimental model for biosecurity pests. PLoS ONE 9(3):e92384. https://doi.org/10.1371/journal.pone.0092384
Holliman FM (2011) Operational protocols for electric barriers on the Chicago Sanitary and Ship Canal: influence of electrical characteristics, water conductivity, fish behaviour, and water velocity on risk for breach by small Silver and Bighead carp. Smith-Root Inc, Vancouver
Honda K, Arai T, Kobayashi S, Tsuda Y, Miyashita K (2012) Migratory patterns of exotic brown trout Salmo trutta in south-western Hokkaido, Japan, on the basis of otolith Sr:Ca ratios and acoustic telemetry. J Fish Biol 80(2):408–426. https://doi.org/10.1111/j.1095-8649.2011.03183.x
Howe EA, Lochet A, Hand CP, Ludsin SA, Marsden JE, Fryer BJ (2013) Discriminating natal origin of spawning adult sea lamprey (*Petromyzon marinus*) in Lake Champlain using statolith elemental signatures. J Great Lakes Res 39(2):239–246. https://doi.org/10.1016/j.jglr.2013.02.006
Hüssy K et al (2020) Trace element patterns in otoliths: the role of biomineralization. Rev Fish Sci Aquacult 29:445–477. https://doi.org/10.1080/23308249.2020.1760204
Izzo C, Reis-Santos P, Gillanders BM (2018) Otolith chemistry does not just reflect environmental conditions: a meta-analytic evaluation. Fish Fish 19(3):441–454. https://doi.org/10.1111/faf.12264
Jerde CL, Mahon AR, Chadderton WL, Lodge DM (2011) "Sight-unseen" detection of rare aquatic species using environmental DNA. Conserv Lett 4(2):150–157. https://doi.org/10.1111/j.1755-263X.2010.00158.x
Jones ML (2007) Toward improved assessment of sea lamprey population dynamics in support of cost-effective sea lamprey management. J Great Lakes Res 33:35–47. https://doi.org/10.3394/0380-1330(2007)33[35:TIAOSL]2.0.CO;2

Jones CM, Palmer M, Schaffler JJ (2016) Beyond Zar: the use and abuse of classification statistics for otolith chemistry. J Fish Biol. https://doi.org/10.1111/jfb.13051

Kalish JM (1989) Otolith microchemistry: validation of the effects of physiology, age and environment on otolith composition. J Exp Mar Biol Ecol 132(3):151–178. https://doi.org/10.1016/0022-0981(89)90126-3

Kelly A, Engle C, Armstrong M, Freeze M, Mitchell A (2011) History of introductions and governmental involvement in promoting the use of grass, silver, and bighead carps. In: Chapman DC, Hoff MH (eds) Invasive Asian Carps in North America. American Fisheries Society, Bethesda

Kinter BT, Jenkins JA, Tyson JT (2018) Assessing the risk of diploid grass carp *Ctenopharyngodon idella* in the certified triploid supply chain in Ohio. J Great Lakes Res 44(5):1093–1099. https://doi.org/10.1016/j.jglr.2018.07.004

Kocovsky PM, Sturtevant R, Schardt J (2018) What it is to be established: policy and management implications for non-native and invasive species. Manag Biol Invasions 9(3):177–185. https://doi.org/10.3391/mbi.2018.9.3.01

Lazartigues AV, Plourde S, Dodson JJ, Morissette O, Ouellet P, Sirois P (2016) Determining natal sources of capelin in a boreal marine park using otolith microchemistry. ICES J Mar Sci 73(10):2644–2652. https://doi.org/10.1093/icesjms/fsw104

Limburg KE, Siegel DI (2006) The hydrogeochemistry of connected waterways: the potential of linking geology to fish migrations. Northeast Geol Environ Sci 28(3):254–265

Limburg KE et al (2015) In search of the dead zone: use of otoliths for tracking fish exposure to hypoxia. J Mar Syst 141:167–178. https://doi.org/10.1016/j.jmarsys.2014.02.014

Lodge DM et al (2006) Biological invasions: recommendations for U.S. policy and management. Ecol App 16(6):2035–54

Love SA, Lederman NJ, Widloe T, Whitledge GW (2019) Sources of bighead carp and silver carp found in Chicago urban fishing program ponds. Trans Am Fish Soc 148(2):417–425. https://doi.org/10.1002/tafs.10142

Macdonald JI, Crook DA (2014) Nursery sources and cohort strength of young-of-the-year common carp (*Cyprinus carpio*) under differing flow regimes in a regulated floodplain river. Ecol Freshw Fish 23(2):269–282. https://doi.org/10.1111/eff.12075

Macdonald J, Crook D, McNeil DG (2010) Identification of carp recruitment hotspots in the Lachlan River using otolith chemistry SARDI Research Report Series. Univesity of Canberra, Canberra, p 27

Maguffee AC, Reilly R, Clark R, Jones ML (2019) Examining the potential of otolith chemistry to determine natal origins of wild Lake Michigan Chinook salmon. Can J Fish Aquat Sci. https://doi.org/10.1139/cjfas-2018-0041

Mercier L et al (2010) Selecting statistical models and variable combinations for optimal classification using otolith microchemistry. Ecol Appl 21(4):1352–1364. https://doi.org/10.1890/09-1887.1

Mercier L, Mouillot D, Bruguier O, Vigliola L, Darnaude AM (2012) Multi-element otolith fingerprints unravel sea-lagoon lifetime migrations of gilthead sea bream *Sparus aurata*. Mar Ecol Prog Ser 444:175–194. https://doi.org/10.3354/meps09444

Morissette O, Sirois P (2020) Flowing down the river: influence of hydrology on scale and accuracy of elemental composition classification in a large fluvial ecosystem. Sci Total Environ 760:143320. https://doi.org/10.1016/j.scitotenv.2020.143320

Morissette O, Lecomte F, Verreault G, Legault M, Sirois P (2016) Fully equipped to succeed: migratory contingents seen as an intrinsic potential for striped bass to exploit a heterogeneous environment early in life. Estuaries Coasts 39(2):571–582. https://doi.org/10.1007/s12237-015-0015-7

Morissette O, Bernatchez L, Wiedenbeck M, Sirois P (2020) Deciphering lifelong thermal niche using otolith δ18O thermometry within supplemented lake trout (*Salvelinus namaycush*) populations. Freshw Biol 65(6):1114–1127. https://doi.org/10.1111/fwb.13497

Morissette O, Lecomte F, Vachon N, Drouin A, Sirois P (2021) Quantifying migratory capacity and dispersal of the invasive Tench (*Tinca tinca*) in the St. Lawrence River using otolith chemistry. Can J Fish Aquat Sci. https://doi.org/10.1139/cjfas-2020-0460

Munro AR, McMahon TE, Ruzycki JR (2005) Natural chemical markers identify source and date of introduction of an exotic species: lake trout (*Salvelinus namaycush*) in Yellowstone Lake. Can J Fish Aquat Sci 62(1):79–87. https://doi.org/10.1139/f04-174

Murayama E, Takagi Y, Ohira T, Davis JG, Greene MI, Nagasawa H (2002) Fish otolith contains a unique structural protein, otolin-1. Eur J Biochem 269(2):688–696. https://doi.org/10.1046/j.0014-2956.2001.02701.x

Nakajima T, Hudson MJ, Uchiyama J, Makibayashi K, Zhang J (2019) Common carp aquaculture in Neolithic China dates back 8,000 years. Nat Ecol Evol 3(10):1415–1418. https://doi.org/10.1038/s41559-019-0974-3

Norman JD, Whitledge GW (2015) Recruitment sources of invasive bighead carp (*Hypopthalmichthys nobilis*) and silver carp (*H. molitrix*) inhabiting the Illinois River. Biological Invasions 17(10):2999–3014. https://doi.org/10.1007/s10530-015-0929-9

North HL, McGaughran A, Jiggins C (2021) Insights into invasive species from whole-genome resequencing. Mol Ecol. https://doi.org/10.1111/mec.15999

Ogden R, Dawnay N, McEwing R (2009) Wildlife DNA forensics—bridging the gap between conservation genetics and law enforcement. Endanger Species Res 9(3):179–195

Pannella G (1971) Fish otoliths: daily growth layers and periodical patterns. Science 173(4002):1124–1127

Patterson WP (1998) North American continental seasonality during the last millennium: high-resolution analysis of sagittal otoliths. Palaeogeogr Palaeoclimatol Palaeoecol 138(1–4):271–303. https://doi.org/10.1016/s0031-0182(97)00137-5

Pracheil BM, Hogan JD, Lyons J, McIntyre PB (2014) Using hard-part microchemistry to advance conservation and management of North American freshwater fishes. Fisheries 39(10):451–465. https://doi.org/10.1080/03632415.2014.937858

Rahel FJ, Smith MA (2018) Pathways of unauthorized fish introductions and types of management responses.

Hydrobiologia 817(1):41–56. https://doi.org/10.1007/s10750-018-3596-x
Rainbow PS (1997) Ecophysiology of trace metal uptake in crustaceans. Estuar Coast Shelf Sci 44(2):169–176. https://doi.org/10.1006/ecss.1996.0208
Ricardo F et al (2015) Trace element fingerprinting of cockle (*Cerastoderma edule*) shells can reveal harvesting location in adjacent areas. Sci Rep 5(1):11932. https://doi.org/10.1038/srep11932
Roloson SD et al (2020) Otolith microchemistry and acoustic telemetry reveal anadromy in non-native rainbow trout (*Oncorhynchus mykiss*) in Prince Edward Island, Canada. Can J Fish Aquat Sci 77(7):1117–1130. https://doi.org/10.1139/cjfas-2019-0229
Rude NP, Yung AJ, Whitledge GW (2017) Movement of small-bodied fishes from Lake Michigan into Chicago Area Waterways: insights from otolith chemistry. J Appl Ichthyol 33(6):1166–1172. https://doi.org/10.1111/jai.13499
Schaeffer JS, Young SP, Herrington S, Ingram T, Tannehill J (2014) Otolith chemistry to determine within-river origins of Alabama shad in the Apalachicola-Chattahoochee-Flint river basin. Trans Am Fish Soc 144:1–10
Secor DH (2013) The unit stock concept: bounded fish and fisheries. In: Cadrin SX, Kerr LA, S M (eds) Stock identification methods: applications in fisheries science. Elsevier Academic Press, London, p 588
Secor DH, Rooker JR (2000) Is otolith strontium a useful scalar of life cycles in estuarine fishes? Fish Res 46:359–371
Secor DH, Henderson-Arzapalo A, Piccoli PM (1995) Can otolith microchemistry chart patterns of migration and habitat utilization in anadromous fishes? J Exp Mar Biol Ecol 192(1):15–33
Spurgeon JJ, Pegg MA, Halden NM (2018) Mixed-origins of channel catfish in a large-river tributary. Fish Res 198:195–202. https://doi.org/10.1016/j.fishres.2017.09.001
Stewart KP, McMahon TE, Koel TM, Humston R (2021) Use of otolith microchemistry to identify subbasin natal origin and use by invasive Lake Trout in Yellowstone Lake. Hydrobiologia 848(10):2473–2481. https://doi.org/10.1007/s10750-021-04568-z
Storm-Suke A, Dempson JB, Caron F, Power M (2007) Effects of formalin and ethanol preservation on otolith delta O-18 stable isotope signatures. Rapid Commun Mass Spectrom 21(4):503–508. https://doi.org/10.1002/rcm.2850
Stuart IG et al (2021) Continental threat: how many common carp (*Cyprinus carpio*) are there in Australia? Biol Cons 254:108942. https://doi.org/10.1016/j.biocon.2020.108942
Sturrock AM et al (2015) Quantifying physiological influences on otolith microchemistry. Methods Ecol Evol 6(7):806–816. https://doi.org/10.1111/2041-210X.12381
Swanson RG, Gagnon JE, Miller LM, Dauphinais JD, Sorensen PW (2020) Otolith microchemistry of Common Carp reflects capture location and differentiates nurseries in an interconnected lake system of the North American Midwest. North Am J Fish Manag 40(5):1100–1118. https://doi.org/10.1002/nafm.10474
Tanner SE et al (2013) Does otolith geochemistry record ambient environmental conditions in a temperate tidal estuary? J Exp Mar Biol Ecol 441:7–15. https://doi.org/10.1016/j.jembe.2013.01.009
Tanner SE, Reis-Santos P, Cabral HN (2016) Otolith chemistry in stock delineation: a brief overview, current challenges and future prospects. Fish Res 173:206–213. https://doi.org/10.1016/j.fishres.2015.07.019
Thibault I, Hedger RD, Dodson JJ, Shiao JC, Iizuka Y, Tzeng WN (2010) Anadromy and the dispersal of an invasive fish species (*Oncorhynchus mykiss*) in Eastern Quebec, as revealed by otolith microchemistry. Ecol Freshw Fish 19(3):348–360. https://doi.org/10.1111/j.1600-0633.2010.00417.x
Thomas ORB, Swearer SE (2019) Otolith biochemistry—a review. Rev Fish Sci Aquacult 27(4):458–489. https://doi.org/10.1080/23308249.2019.1627285
Vu AV et al (2021) Variability in water chemistry in the Lower Mekong Basin: considerations for fish life history reconstruction. Estuar Coast Shelf Sci 255:107355. https://doi.org/10.1016/j.ecss.2021.107355
Walther BD (2019) The art of otolith chemistry: interpreting patterns by integrating perspectives. Mar Freshw Res 70:1643–1658. https://doi.org/10.1071/MF18270
Walther BD, Thorrold SR (2006) Water, not food, contributes the majority of strontium and barium deposited in the otoliths of a marine fish. Mar Ecol-Prog Ser 311:125–130. https://doi.org/10.3354/meps311125
Wells BK, Rieman BE, Clayton JL, Horan DL, Jones CM (2003) Relationships between water, otolith, and scale chemistries of Westslope Cutthroat Trout from the Coeur d'Alene River, Idaho: the potential application of hard-part chemistry to describe movements in freshwater. Trans Am Fish Soc 132(3):409–424. https://doi.org/10.1577/1548-8659(2003)132%3c0409:RBWOAS%3e2.0.CO;2
Whitledge GW, Johnson BM, Martinez PJ, Martinez AM (2007) Sources of nonnative centrarchids in the Upper Colorado River revealed by stable isotope and microchemical analyses of otoliths. Trans Am Fish Soc 136(5):1263–1275. https://doi.org/10.1577/T06-045.1
Whitledge GW et al (2019) Identification of bighead carp and silver carp early-life environments and inferring Lock and Dam 19 passage in the Upper Mississippi River: insights from otolith chemistry. Biol Invasions 21:1007–1020. https://doi.org/10.1007/s10530-018-1881-2
Whitledge GW et al (2021) Identifying sources and year classes contributing to invasive grass carp in the Laurentian Great Lakes. J Great Lakes Res 47(1):14–28. https://doi.org/10.1016/j.jglr.2020.07.008
Williams SB (2013) Use of stable isotope and trace metal signatures to track the emigration of female blue crabs, *Callinectes sapidus*, from Tampa Bay. University of South Florida, Tampa
Williams JA, Whitledge GW, Knights BC, Bloomfield NC, Lamer JT (2021) Age-0 Silver Carp otolith microchemistry and microstructure reveal multiple early-life environments and protracted spawning in the Upper Mississippi River. N Am J Fish Manag. https://doi.org/10.1002/nafm.10707
Wolff AB, Johnson Brett M, Breton André R, Martinez Patrick J, Winkelman Dana L (2012) Origins of invasive

piscivores determined from the strontium isotope ratio (87Sr/86Sr) of otoliths. Can J Fish Aquat Sci 69(4):724–739. https://doi.org/10.1139/f2012-009

Wright PJ, Régnier T, Gibb FM, Augley J, Devalla S (2018) Assessing the role of ontogenetic movement in maintaining population structure in fish using otolith microchemistry. Ecol Evol 8(16):7907–7920. https://doi.org/10.1002/ece3.4186

Zajicek P, Goodwin AE, Weier T (2011) Triploid grass carp: triploid induction, sterility, reversion, and certification. N Am J Fish Manag 31(4):614–618. https://doi.org/10.1080/02755947.2011.608616