Using otoliths for fish stock discrimination: status and challenges

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Abstract

Otoliths are calcified structures and the information contained within their chemistry or shape can be used to infer life history events, migration patterns, and stock structure of a fish population. Understanding how otolith chemistry is affected by temperature, salinity, interactive effects of abiotic factors, ontogeny, physiology, etc. is essential for the reconstruction of the environment that affected the fish. Otolith shape is also affected by environmental conditions in addition to the genotype. The applications of otolith chemistry and shape for stock discrimination have increased in recent years because of the advancements in analytical methods and the related software. The stock identification methods sometimes provide variable results but if we use complementary approach the information generated could be more reliable which can be used to prepare effective management and conservation strategies. It appears warranted to generate more information on the factors influencing otolith chemistry and shape especially when two or more factors exert synergetic influence. Therefore, the objectives of this review paper were to provide comprehensive information on various factors influencing the otolith chemistry and shape, and the utility of otolith chemistry and shape for fish stock discrimination with an emphasis towards the research areas needing additional studies.

Keywords

Introduction

Otoliths are calcified biominerals that are mainly composed of calcium carbonate polymorph aragonite and a minor quantity of biomolecules such as proteoglycans and glycoproteins (Campana 1999; Sollner et al. 2003). The process of otolith biomineralization is influenced by several genes and the fish may also use collagens to stimulate biogenesis (Murayama et al. 2002; Sollner et al. 2003). Moreover, it is reported that otolin-1 (mesh-work-forming collagen) may contribute to forming biominerals composed of calcium carbonate (Murayama et al. 2002). The mineralized calcium carbonate is precipitated from the endolymph fluid which contains calcium and bicarbonate ions and it is reported that there is a daily pause in deposition caused by changes in endolymph pH cycles (Wright et al. 1992; Campana and Thorrold 2001). Thus, the chemical composition of endolymph surrounding otolith is an important factor for otolith growth.

Otolith chemistry reflects the permanent record of physical and chemical qualities of the ambient environment (Campana 1999). The whole dissolved otolith composition reveals the average of the lifetime exposure to both the ambient environment and its physiological processes thus delineating based on differences among the groups of fishes exposed to different environments (Campana et al. 2000). The variations in the elemental composition of whole otoliths cannot be used to infer the time period when the groups of fishes remained separated because the arbitrary inhabitancy in different environmental

conditions can lead to an evident change in the otolith elemental composition (Campana 2005). The application of beam-based instruments such as laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS) has revolutionized the understanding of temporal patterns in otolith composition (Di Franco et al. 2014).

Several studies have reported that the otolith chemistry is influenced by environmental factors (e.g., water chemistry, temperature, salinity, and their interactive effects) and physiological processes (e.g., growth, metabolism, and reproductive stage) (Elsdon and Gillanders 2003; Gaetani and Cohen 2006; Walther et al. 2010; Sturrock et al. 2014; Stanley et al. 2015; Mazloumi et al. 2017; Walsh and Gillanders 2018). Therefore, the knowledge of how exogenous and endogenous factors affect otolith chemistry is essential to reconstruct the life history events and the migration pattern of fish species (Elsdon et al. 2008; Reis-Santos et al. 2013). The predominant source of the elements incorporated into the otoliths is the ambient water but for some elements such as Zn the main source is diet thereby the relative contribution may vary for different elements (Walther and Thorrold 2006; Doubleday et al. 2013). The ambient water chemistry is regulated by several factors such as underlying geology, anthropogenic influences, precipitation, agricultural runoff, mixing of different water bodies, etc. (Elsdon et al. 2008). Therefore, the chemical composition may vary between water bodies or even within a water body at temporal and spatial scales (Kerr et al. 2007; Elsdon et al. 2008). Moreover, otoliths permanently record spatial and temporal variability in water chemistry (Campana et al. 2000; Dorval et al. 2005; Miller 2007; Mateo et al. 2010).

The shape of otoliths is species-specific and shows less variation in growth comparative to somatic growth (Campana and Casselman 1993; Lombarte and Lleonart 1993). Otolith shape variation of fish from different geographic areas is supposed to provide evidence that the fish species occupied distinct regions during life history, thus demonstrating a phenotypic method of stock identification (Ihssen et al. 1981). Otolith shape is a more reliable tool because it is comparatively more stable than external morphometric characters to the short-term variations caused by changes in fish condition (feeding or spawning conditions) or environmental variations (Vieira et al. 2014; Mahe et al. 2018). Several studies have reported that the variations in otolith shape may be correlated with differences in growth rate (Campana and Casselman 1993), as noted in Atlantic mackerel, *Scomber scombrus* Linnaeus, 1758 (see Castonguay et al. 1991); king mackerel, *Scomberomorus cavalla* (Cuvier, 1829) (see DeVries et al. 2002); and blue whiting, *Micromesistius poutassou* (Risso, 1827) (see Keating et al. 2014). Vignon and Morat (2010) reported that the left and right otoliths are influenced symmetrically by the environment and genetics. This may have key implications because any unsystematic deviations from perfect symmetry of otoliths may be used to study the developmental stress and hence could be a potential sign of fitness (Lemberget and McCormick 2009; Palmer et al. 2010).

Several studies have used otolith chemistry (Edmonds et al. 1991; Campana et al. 1994; Campana 2005; Volpedo and Cirelli 2006; Pangle et al. 2010; Khan et al. 2012; Khemiri et al. 2014; Miyan et al. 2014; Miyan et al. 2016; Avigliano et al. 2017; Moreira et al. 2018; Wright et al. 2018; Nazir and Khan 2019) or shape of otoliths (Campana and Casselman 1993; Begg and Brown 2000; DeVries et al. 2002; Pothin et al. 2006; Stransky et al. 2008; Aguera and Brophy 2011; Keating et al. 2014; Sadighzadeh et al. 2014; Vieira et al. 2014; Bacha et al. 2016; Ider et al. 2017; Khemiri et al. 2018) as a tool for stock discrimination. However, the understanding of the ecological and evolutionary processes that sustain the fish population structure requires a multidisciplinary approach (Abaunza et al. 2008; Taillebois et al. 2017). Therefore, the environmental markers (e.g., otolith microchemistry) and genetic markers may provide important information to assess stock structure especially if they show high agreement when used in union (Welch et al. 2015; Tanner et al. 2016). Several researchers have concurrently used otolith chemistry and shape to indirectly validate the percentage of correct classification of individuals to their original location(s) (Turan 2006; Longmore et al. 2010; Ferguson et al. 2011; Soeth et al. 2019). Further, it is preferable to conduct similar investigations to generate conclusive information on population structure and to assess the generality of the results (Longmore et al. 2010).

Several review papers based on otolith chemistry have been published both at the global and regional level (Campana 1999; Campana and Thorrold 2001; Elsdon and Gillanders 2003; Elsdon et al. 2008; Sturrock et al. 2012; Pracheil et al. 2014; Avigliano and Volpedo 2016; Tanner et al. 2016; Walther et al. 2017; etc.). However, more information is warranted on all exogenous and endogenous factors influencing otolith chemistry and shape. Therefore, the objectives of this review paper were to provide comprehensive information on various factors influencing the otolith chemistry and shape, and the utility of otolith chemistry and shape for fish stock discrimination with an emphasis towards the research areas needing additional studies.

Factors affecting otolith chemistry

Otolith chemistry reflects the habitat conditions at different life-history stages of a fish species (Elsdon and Gillanders 2003). The geographic variations in the ambient environmental conditions may result in regional patterns in otolith chemistry (Chang and Geffen 2013) and significant differences in otolith chemistry at spatial scales were reported (Kennedy et al. 2005; Miyan et al. 2016; Wright et al. 2018; Nazir and Khan 2019). The taxonomic relations or ecological resemblances between fish species may result in phylogenetic patterns in otolith chemistry

(Chang and Geffen 2013), thereby limiting the implementation of a single common model (Martin and Wuenschel 2006). The physiological regulation has a greater impact on otolith chemistry particularly when the source of elements is other than water (Walther et al. 2017). Therefore, a complete understanding of exogenous and endogenous factors and their relative effects on the accretion of elements in otolith is needed (Izzo et al. 2018).

Effect of temperature

Temperature variations at both spatial and temporal scales influence otolith chemistry because it affects precipitation reactions of trace elements. Morse et al. (2007) reported that the solubility of all pure carbonates decreases with increasing temperature. Temperature affects the crystal precipitation process because it influences the pH of the blood plasma and endolymph fluid (Romanek and Gauldie 1996; Elsdon and Gillanders 2003). The complete information of the life history events and the migration pattern of the fish species may be possible by understanding the relation between temperature and otolith chemistry (Mazloumi et al. 2017). Previously, several studies through controlled experiments have reported the effects of temperature on otolith chemistry (Miller 2009; DiMaria et al. 2010; Reis-Santos et al. 2013). Moreover, a number of studies have reported the effects of temperature on otolith chemical composition, which has produced both positive and negative effects of temperature on otolith chemistry (DiMaria et al. 2010; Barnes and Gillanders 2013; Reis-Santos et al. 2013; Stanley et al. 2015; Walsh and Gillanders 2018). The variations in the results may be due to the temperature ranges used in the experiments which were generally narrower than the fish typically experience in nature (Elsdon and Gillanders 2003; Reis-Santos et al. 2013). Recently, Izzo et al. (2018) reported that the experiments undertaken at low temperature (<5°C) or short duration experiments (<20 days) produced varying results, thus emphasizing that the experimental conditions may have an influential effect on the final conclusion of the study. Therefore, it is suggested to undertake future experiments at different life stages and by keeping in view the temperature conditions experienced by the fish species under natural conditions (Sturrock et al. 2012; Sturrock et al. 2015; Izzo et al. 2018).

Several studies have reported the effects of temperature on otolith chemistry, but a full understanding of the relation is lacking because it is complicated by other factors that affect otolith chemistry (such as salinity, diet, species-specific physiology, etc.) and many empirical studies do not replicate the range of conditions that the species of interest experience naturally (Sturrock et al. 2012; Barnes and Gillanders 2013; Walsh and Gillanders 2018). Therefore, it is required that more studies should be undertaken to validate and evaluate the temporal environmental changes which influence otolith chemistry

(Miller 2011) and to examine the mechanism through which temperature affects otolith chemistry across a full reproductive cycle (Sturrock et al. 2012; Reis-Santos et al. 2013).

During the assessment of the literature, we found some specific study designs that were particularly good to understand the factors influencing the otolith chemistry, for example, Sturrock et al. (2015) carried out a 1-year controlled experiment across immature and mature reproductive stages of European plaice, *Pleuronectes platessa* (Linnaeus, 1758), at nearly natural conditions to assess the influence of environmental and physiological variables to establish a basis for modeling the uptake and transport pathways of elements to the otoliths. In another controlled laboratory experiment on the fingerlings of mulloway, *Argyrosomus japonicus* (Temminck et Schlegel, 1843), the temperature and salinity ranges were set similar to the natural conditions to study the influence of environment and genetics on the chemical composition of otoliths with a caution that a range of environmental conditions to which the fish may be exposed should be considered (Barnes and Gillanders 2013). The elements such as Sr, Ba, and Mn are the most frequently used elemental markers in otolith chemistry studies based on a positive correlation between incorporation rates, ambient concentrations, and/or temperature (Reis-Santos et al. 2013; Sturrock et al. 2015).

Effect of salinity

Salinity changes occur due to precipitation and evaporation processes within water bodies, leading to a stratification of the water column which often delimits boundaries between different water bodies (Tomczak and Godfrey 1994). Mucci (1983) investigated the effect of salinity on the stoichiometric solubility products and reported that the solubility products of aragonite tend to increase with increasing salinity. It is also described that the aragonite precipitation rates tended to decrease (about five times) with increasing salinity, although this decrease was only observed for salinity ≥ 35‰ (Zhong and Mucci 1989). The uptake of elements from blood-endolymph-otolith is affected by salinity (McCormick 2001). In the case of highly migratory fish species (diadromous species), which moves across different salinity environments, the gill membrane osmoregulates the movement of ions (Miller 2011; Sturrock et al. 2012). Thus, the understanding of the effects of salinity on otolith chemistry is very essential to study the migration pattern of fish species. The influence of salinity on elements such as Sr and Ba has been frequently studied in deciphering the migration between habitats exhibiting strong gradients of salinity (Milton and Chenery 2005; Reis-Santos et al. 2013).

Several studies have reported strong positive and negative effects of salinity on otolith chemistry (Kraus and Secor 2004; Dorval et al. 2007; Sturrock et al. 2012; Reis-Santos et al. 2013; Panfili et al. 2015; Mazloumi et

al. 2017; Walsh and Gillanders 2018). A number of studies also reported no significant effect of salinity on Sr, Ba, Mg, and Mn concentrations in the otoliths (Elsdon and Gillanders 2002; Elsdon and Gillanders 2005; Martin and Wuenschel 2006; Gillanders and Munro 2012). This disagreement of results suggests that other factors may interact with salinity to affect the elemental incorporation and also, the salinity does not influence all elements equally and concurrently; consequently, the species may accrete elements within their otoliths in different ways (Elsdon and Gillanders 2003). Several reasons may explain this disagreement or complexity of the results. The elements such as Ba, Sr, Mn, Mg, and Li are mainly found as hydrated free ions both in seawater and blood, and these ions are relatively constant in seawater and mostly vary with salinity changes (Sturrock et al. 2012). Moreover, the physiological processes, the kinetic growth effect, and the synthesis of protein throughout somatic growth are the pivotal factors that affect the ion uptake into otoliths (Sinclair 2005; Trudel et al. 2010; Sturrock et al. 2012). The Dynamic Energy Budget Models (e.g., biokinetic and bioenergetic models) can be used to further investigate a suite of environmental and/or biological factors to evaluate the rate of uptake of individual elements (Fablet et al. 2011; Izzo et al. 2018). Thus, additional validation experiments are needed to understand the influence of salinity and other abiotic and biotic factors influencing the incorporation rate of individual elements into otoliths (Reis-Santos et al. 2013).

Interactive effects of temperature and salinity

The water chemistry, temperature, and salinity are the three key environmental factors influencing the otolith chemistry and these variables are usually not independent of each other (Elsdon and Gillanders 2003). The temperature and salinity have a significant influence on the otolith chemistry especially in estuaries where more than one factor can vary (Elsdon et al. 2008). Several studies have reported that the Ba:Ca ratio usually shows positive and negative relation with temperature and salinity, respectively (Elsdon and Gillanders 2005; Dorval et al. 2007; Marohn et al. 2011; Reis-Santos et al. 2013; Stanley et al. 2015; Mazloumi et al. 2017; Nelson and Powers 2019). The Sr:Ca ratio generally shows positive relation with both temperature and salinity (Bath et al. 2000; Zimmerman 2005; Martin and Wuenschel 2006; Brown and Severin 2009; Miller 2009; Reis-Santos et al. 2013; Mazloumi et al. 2017; Nelson and Powers 2019). Further, the Mn:Ca and Mg:Ca usually show no relation with temperature and salinity (Elsdon and Gillanders 2002; Martin and Thorrold 2005; Tanner et al. 2011; Gillanders and Munro 2012; Mazloumi et al. 2017). Therefore, the interactive influence of temperature and salinity should be considered for accurate reconstruction of the

environmental history of fish species (Elsdon et al. 2008; Miller 2011).

Laboratory-based validation experiments have been performed to analyse the accretion of elements on the otoliths for a number of species, but a limited number of studies have examined the interactive effect of temperature and salinity (Walsh and Gillanders 2018). Therefore, the interpretation of environmental histories of fishes based on single environmental factor may provide imprecise information as the elements are possibly confounded by the effect of other variables thereby highlighting the importance of studying interactive effects of environmental factors (Martin and Wuenschel 2006). Moreover, the interactive effects of environmental variables may also represent species-specific responses to these variables (Tzeng 1996; Chesney et al. 1998). Evaluating the interactive effect of temperature and salinity on otolith chemistry by using a multi-element approach can enhance our interpretation of migration patterns and stock assessment (Elsdon and Gillanders 2003).

Effect of crystal structure

Several studies have reported that the otoliths vary considerably in the crystal structure and the differences in elemental composition were found among $CaCO_3$ polymorphs (Melancon et al. 2005; Tzeng et al. 2007; Ma et al. 2008; Veinott et al. 2009). All the elements which are incorporated from the water into the aragonite and vaterite do not follow the same pattern (Pracheil et al. 2017). Typically, the vaterite contains lower elemental concentrations than aragonite (Pracheil et al. 2019). The elements such as Sr and Ba have lower elemental concentrations in vaterite portions than aragonite portions, for example, the otoliths of European eel, *Anguilla anguilla* (Linnaeus, 1758) (see Tzeng et al. 2007). Further, the elements such as Mg and Mn have increased concentrations in vaterite compared to aragonite sections, for example, the otoliths of lake trout, *Salvelinus namaycush* (Walbaum, 1792) (see Melancon et al. 2005), brown trout, *Salmo trutta* (Linnaeus, 1758), and brook charr, *Salvelinus fontinalis* (Mitchill, 1814) (see Morat et al. 2008). Moreover, it is reported that aragonite otolith chemistry reflects water chemistry whereas vaterite otolith chemistry does not reflect ambient water chemistry thereby vaterite otoliths may be of limited use in stock identification and reconstructing the environmental history of fishes (Bath et al. 2000; Gillanders and Kingsford 2000; Pracheil et al. 2017). Usually, otoliths have aragonite or vaterite crystal structure, however, Campana (1983) first documented the coprecipitation of aragonite and vaterite in the same otolith but at different growth zones and later it was reported that the environmental stress and/or changes within soluble proteins of the endolymph are mainly responsible for this to occur especially in hatchery-reared fishes (Sweeting et al. 2004; Tomas et al. 2004; Ma et al. 2008; Morat et al. 2008). Gauldie (1986) reported that the water temperature

was a prime cause in producing a shift between aragonite and vaterite in otoliths of chinook salmon, *Oncorhynchus tshawytscha* (Walbaum, 1792). Aragonite and vaterite otoliths differ in their densities and lattice structure; vaterite is less dense than aragonite (Tomas and Geffen 2003; Chakoumakos et al. 2016; Neves et al. 2017), resulting in otolith mass asymmetry (Vignon and Aymes 2020). The vaterite precipitation has a negative impact on auditory sensitivity in fishes (Reimer et al. 2016). Moreover, the functional, behavioural, and ecological implications of vaterite deposition at the organismal level are usually untested experimentally (Vignon and Aymes 2020). The calcium and other trace element concentrations may vary from one polymorph to another thereby the data should be normalised accordingly otherwise it will lead to inaccurate results (Pracheil et al. 2017). To increase the accuracy of the otolith chemistry technique, there is a need to understand the link between calcium polymorphs and incorporation rate of elements, and the occurrence of several calcium polymorphs across the hatchery-reared and wild fish species (Pracheil et al. 2019).

Effects of growth, diet, and ontogeny

The growth rate of a fish species is known to influence the elemental incorporation in otolith (Martin and Thorrold 2005; Sturrock et al. 2012). Further, it is reported that the individuals which live in the same water body may have different otolith compositions if they exhibit different growth rates (DiMaria et al. 2010). However, several studies have reported that the chemical composition of otoliths usually shows a negative or no relation with growth (Bath et al. 2000; Martin et al. 2004; Martin and Thorrold 2005; Lin et al. 2007; Miller 2009). The variations in growth rate among the groups of fish should be determined if whole otoliths are analysed (Elsdon et al. 2008). Thus, it is necessary that the fish of known or same sex, size, and age should be collected among areas for analysis (Wells et al. 2003; Sturrock et al. 2012). In general, two hypotheses have been put forward, such as the kinetic and the physiological hypothesis to explain the influence of growth rate differences on the accretion of elements in otoliths (Walther et al. 2010). The kinetic hypothesis describes the calcification rate such as precipitation and substitution in the otolith (Sinclair 2005). Also, the kinetic hypothesis suggests that the pH influences the level of calcium concentration in the endolymph and it also changes the relative abundance of bivalent ions in the calcifying fluid especially when the incorporation rate is fast (Sinclair 2005; Sinclair and Risk 2006). Kinetic hypothesis needs to be completely resolved experimentally, because of the incongruities among the kinetic hypothesis models of calcification (Walther et al. 2010). A fish species physiologically change the relative concentration of ions during transport

across interfaces from the ambient environment to crystal lattice (Campana 1999; Walther et al. 2010). However, the majority of the studies focus on the applicability of otolith chemistry instead of mechanisms of incorporation of elements in otoliths (Hussy et al. 2020). The physiological processes (e.g., growth) are known to affect the otolith chemistry and it is known that the faster growth rate could alter the concentration of ions in endolymph because of protein synthesis especially calcium-binding proteins during somatic growth (Trudel et al. 2010; Walther et al. 2010). The growth rate is the most important factor among physiological factors that show significant relation with otolith chemistry (Stanley et al. 2015). Furthermore, the growth rate effects confound efforts to spatially discriminate fishes based on the variations in otolith chemistry; therefore, to understand the influence of growth rate on the composition of otoliths further studies should be undertaken to elucidate its effects. The elemental incorporation in otoliths is highly element-specific and varies among life history stages, species, and ecosystems (Hussy et al. 2020) therefore, it is in general difficult to separate and identify the respective roles of kinetic and physiological hypotheses.

The elemental signatures in otoliths are accreted usually from water but the effect of diet is also significant for few elements such as Sr and Ba (Woodcock et al. 2012; Doubleday et al. 2013; Woodcock and Walther 2014). Several studies reported that the diet influences Sr and Ba concentration in otoliths of freshwater, marine, and estuarine fish species by manipulating diet; though, the reported results show contradiction (Hoff and Fuiman 1995; Limburg 1995; Milton and Chenery 2001; Buckel et al. 2004; Marohn et al. 2009; Engstedt et al. 2012). Tanner et al. (2016) reported that the diet shifts with life history stages in the same habitat, or when individuals from geographically distinct populations feed on different preys, show different otolith compositions. The bioaccumulation of elements during the dietary shift towards higher trophic level makes it very difficult to evaluate the influence of diet on otolith chemistry (Gray 2002). Other than water chemistry and diet, several factors may affect otolith chemistry at varying degrees such as fish species, temperature, salinity, growth rate, ontogeny, etc. The combined effect of these variables is seldom tested and may obscure the relative contributions of water chemistry and diet (Doubleday et al. 2013).

Otolith chemistry can vary with life history stages (growth from larval to juvenile and juvenile to adult stages) and metamorphosis (Toole et al. 1993; Elsdon and Gillanders 2003). If the variations in otolith chemistry of a fish species bridge with life-history stages then the elemental profile of otoliths may be a reflection of ontogenetic effects rather than changes in the environmental conditions (Elsdon et al. 2008). Fish species such as eels show metamorphosis thereby are very susceptible to ontogenetic changes in the chemical composition of otoliths which could be misinterpreted as migration patterns (Arai et al. 2002; Correia et al. 2003). To understand

how ontogeny affects otolith chemistry, validation experiments by rearing fish at constant or known environmental conditions during ontogenetic and/or physiological changes (Fowler et al. 1995; Elsdon and Gillanders 2005; Zimmerman 2005) can elucidate such effects.

Other factors affecting otolith chemistry

Stress can influence otolith chemistry but the trend and mechanism driving such results are still not clearly known (Kalish 1992; Walther et al. 2010). Mohan et al. (2014) hypothesized that hypoxic stress can affect otolith chemistry because of physiological changes in blood chemistry resulting from changes in blood proteins. Further, the authors observed without a clear mechanism that constant hypoxia exposure over few weeks does not affect otolith chemistry whereas the periodic hypoxia influences otolith chemistry in Atlantic croaker, *Micropogonias undulatus* (Linnaeus, 1766). Manganese can be used as an environmental indicator to study hypoxic stress because Mn:Ca ratio is not affected by endogenous hypoxic stress (Mohan et al. 2014; Limburg et al. 2015). Laboratory validation experiments are required to address the mechanism underlying the effect of stress on otolith chemistry.

The reproductive conditions can influence the ion transport, flux of elements into the blood plasma, and consequently the availability of elements for uptake into otolith (Sturrock et al. 2014). Laboratory experiments separating their influences from other prominent factors such as temperature, salinity, and growth could provide critical evidence for the accurate interpretation of uptake into otolith (Sturrock et al. 2014). Further work is warranted to experimentally address the effect of a full reproductive cycle on the otolith chemistry.

Factors affecting otolith shape

The exogenous and endogenous factors determine the shape of otoliths and these variables may change between populations thereby resulting in stock-specific characteristics of otoliths (Campana and Neilson 1985). However, a complete understanding of the environmental and genetic factors which determine otolith shape is lacking (Vignon and Morat 2010). Several studies have reported that both genetic and environmental influences may be responsible for otolith shape variations in a particular fish species (Cardinale et al. 2004; Burke et al. 2008; Vignon and Morat 2010). However, few empirical studies have investigated the influence of both environmental and genetic factors on otolith shape. For example, Cardinale et al. (2004) released hatchery cod, *Gadus morhua* Linnaeus, 1758, into the wild and after some years recaptured the species to validate the genetic and environmental influences on the otolith shape. Hus-

sy et al. (2016a) reported the combined effect of environment, ontogenetic and genetic influence on otolith shape of Baltic Sea cod, *Gadus morhua*. Several studies have suggested that local environmental conditions are responsible for otolith shape variations in absence of genetic differences (Simoneau et al. 2000; Katayama and Isshiki 2007; Legua et al. 2013). The introduction of non-native fish species having distinct evolutionary history and genetics could provide a remarkable method to analyse both genetic and environmental influence on otolith shape particularly when the species were introduced in the same habitat (Vignon and Morat 2010). The environmental conditions, genetics, and their interaction may act symmetrically on both left and right otolith thereby carrying the same kind of information (Vignon and Morat 2010). Additional studies should be undertaken to elucidate the effects of other confounding factors such as sex, size, age, stock, food availability, temperature, etc. on the shape of otoliths.

Several studies have reported abnormal otoliths which have different size, shape, and density as compared to normal otoliths in a number of freshwater and marine fishes (Sweeting et al. 2004; Oxman et al. 2007; Ma et al. 2008; Reimer et al. 2016). In the case of abnormal otoliths, the aragonite is replaced by vaterite but in some species, calcite may replace aragonite (Gauldie 1993; Campana 1999; Ma et al. 2008; Reimer et al. 2017). Various factors are responsible for aberrant otoliths such as stress, genetic and neuroendocrine factors but a limited number of studies have tested the effect of these factors (Tomas et al. 2004; Ma et al. 2008; Reimer et al. 2017). The replacement of aragonite by vaterite is usually higher in fish species that are hatchery-reared but this may also occur in wild fishes (Tomas and Geffen 2003). Currently, there are high incidences of culture fishes entering into the natural water bodies; therefore, it becomes necessary to evaluate otolith abnormality and to verify its effects before analyzing otolith shape for fish stock discrimination.

Diet is also known to influence otolith shape because the composition of the diet may affect saccular endolymph proteins which play an essential role in otolith biomineralization (Mille et al. 2016). However, there is a paucity of information regarding the relation between diet and otolith shape. Oceanic acidification is known to change the carbonate structure morphologically in invertebrates and fish otoliths (Checkley et al. 2009; Bignami et al. 2013; Reveillac et al. 2015). Mirasole et al. (2017) reported the effects of ocean acidification on otolith shape and suggested that the fish species which show high site fidelity/territorial behaviour are more influenced as compared to pelagic and more mobile species. The effect of ocean acidification on otolith shape depends on exposure time, levels of CO_2, and species behaviour (Munday et al. 2011). The complete understanding of the variations in otolith shape on fish physiology and behavior needs further investigation in acidified oceans (Munday et al. 2014; Mirasole et al. 2017).

Otoliths as a tool in stock discrimination

Otolith chemistry

Traditionally, the artificial tagging of fish and telemetry are applied to study the life history events (Landsman et al. 2011). The main challenges with tagging are the high investment required (both in costs and human time) and the comparatively small resulting amount of data collected. Even if tagging is cheaper there is still the issue of diminishing returns of tagged individuals (Carlson et al. 2017). Currently, the information contained within otolith chemistry has been used to infer the stock structure and environmental history of the fish species (Clarke et al. 2007; Allen et al. 2009; Reis-Santos et al. 2018). The otolith chemistry has been effectively used to identify the natal origin or dispersal pattern of a number of marine, freshwater, and anadromous fishes (Schaffler and Winkelman 2008; Zeigler and Whitledge 2010; Turner and Limburg 2014; Bailey et al. 2015; Garcez et al. 2015). A major disadvantage of using otolith chemistry is the temporal variability in water chemistry within the natal origin of fish populations (Pangle et al. 2010). Moreover, large temporal variations may restrict the use of otolith chemistry for stock discrimination of fish populations of several age classes because it may influence the classification accuracy at spatial scales (Hamer et al. 2003;

Dorval et al. 2005; Pangle et al. 2010). Therefore, it is suggested to construct an annual baseline of water chemistry and otolith chemistry signatures of cohorts of known origin to assess variability over time.

The utility of otolith chemistry for stock discrimination has risen effectively in the past two decades. The otolith chemistry and its utility in stock discrimination have appeared in nearly 1500 peer-reviewed papers from 2000 to 2019 (Web of Science™, search on 17 September 2020; search term: otolith chemistry OR otolith microchemistry OR otolith elemental composition (black bar), and otolith chemistry OR otolith microchemistry OR otolith elemental composition AND stock discrimination OR stock delineation OR stock deciphering (grey bar)). Approximately 39% of these papers were published in the past five years and the number of papers based on this parameter is increasing with time (Fig. 1). Jonsdottir et al. (2006b) used otolith elemental composition to study the stock structure of Icelandic cod, *Gadus morhua*. Moreover, the otolith chemistry (especially Ba, Li, and Sr at all locations) showed differences in the spawning area of cod in the north and south of Iceland. Similarly, the spawning cod showed different otolith chemistry in the south of Iceland at the main spawning ground below and above 125 m depth. The Icelandic cod was managed as a single stock; however, several studies have indicated more than two stock residing north and south of Iceland by using a holistic approach such as otolith shape and insights from microsatellites, Syp I locus, Pan I locus, and tag-
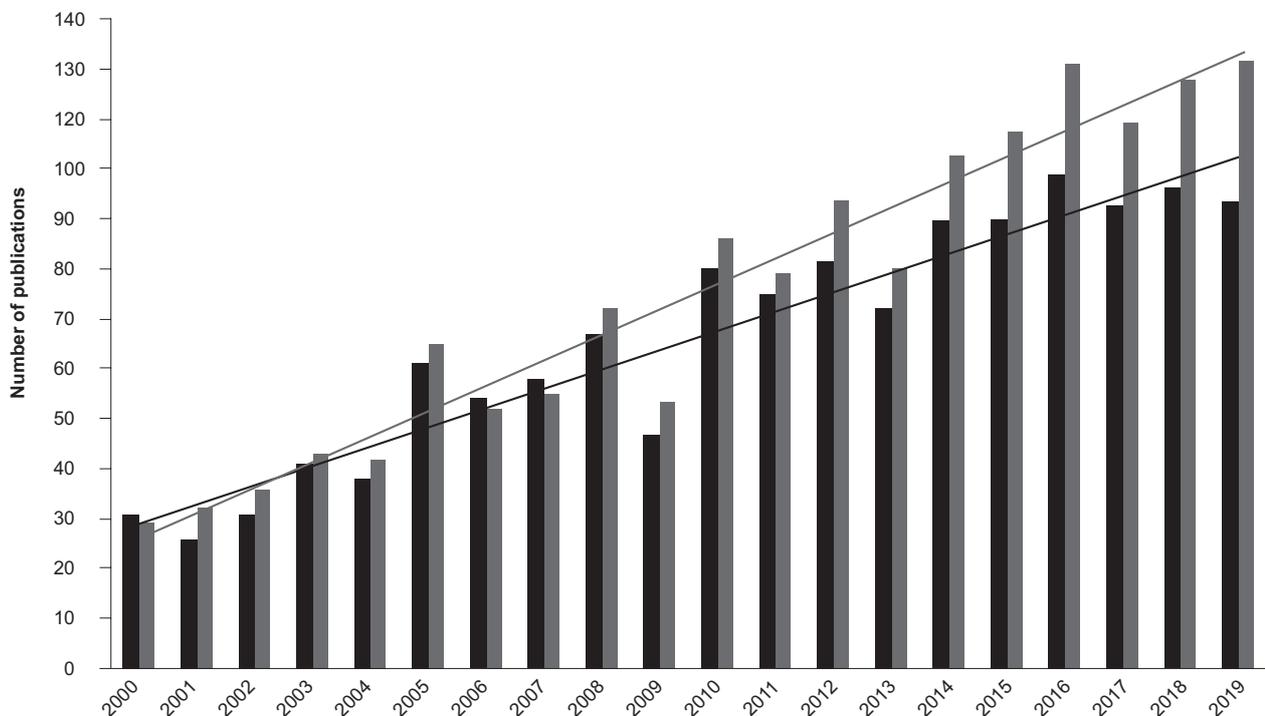

Figure 1. Number of publications per year featuring otolith chemistry (Web of Science, search on 17 September 2020, search term: otolith chemistry OR otolith microchemistry OR otolith elemental composition (black bar), and otolith chemistry OR otolith microchemistry OR otolith elemental composition AND stock discrimination OR stock delineation OR stock deciphering (grey bar)). Lines indicate the trends and results were not cross-checked.

ging experiments (Jonsdottir et al. 2002; Jonsdottir et al. 2006a, 2006b; Pampoulie et al. 2006; Petursdottir et al. 2006). The management strategies developed for a single cod stock around Iceland is not effective because the connectivity of the cod populations (northeast and southwest) and the migration to and from feeding grounds were not taken into consideration (Pampoulie et al. 2012). Dou et al. (2012) reported that the otolith chemistry of tapertail anchovy, *Coilia nasus* Temminck et Schlegel, 1846 varied considerably among five Chinese estuaries (Liaohe River estuary, the Haihe River estuary, the Yellow River estuary, the Daguhe River estuary, and the Yangtze River estuary). They observed that the Sr and Ba composition in the otolith nuclei exhibited inter-site differences and can be used as a successful natural marker for discriminating stocks with an overall classification accuracy rate of 72.7%. Although, the authors recommended that further studies on the interactions of environmental factors in the spawning sites as well as the physiological effects on the elemental uptake into the otoliths are necessary. Miyan et al. (2016) reported that the variations in Sr, Ba, Li, Cu, Fe, Pb, Zn, Mn, Ni, and Mg were important to isolate the stocks of the giant river-catfish, *Sperata seenghala* (Sykes, 1839), in the Gangetic River system (rivers Ganga, Yamuna, and Gomti) with a mean classification accuracy of 83.2%. Moreover, site-specific elemental variances in *S. seenghala* otoliths showed a high level of fidelity to its feeding/growing area. Furthermore, the barrages at Narora and Kanpur locations along the Ganga River could have restricted the movement which consequently could have led to the stock separation in the Ganga River. The microsatellite markers showed different populations of the giant river catfish among the rivers Ganga, Brahmaputra, Godavari, Mahanadi, and Narmada, and therefore separate management plans should be formulated for these populations (Acharya et al. 2019). Wright et al. (2018) reported that in the North Sea, the lesser sandeel, *Ammodytes marinus* (Raitt, 1934), shows significant spatial differences in otolith chemistry although overall classification accuracy was low (48.8%). Further, the elements such as Mn and Rb were important in stock discrimination of *A. marinus* and likely reflect the physico-chemical environment. The authors also reported that the *A. marinus* is currently managed as seven stocks discriminated based on biophysical model predictions of the restricted larval mixing among the stocks. It is reported that the lesser sandeel shows weak genetic differentiation although strong functional genomic signal in the North Sea, however, the use of several genetic markers can increase the power to characterize the genetic population structure (Jimenez-Mena et al. 2020). Nazir and Khan (2019) reported site-specific four stocks of long-whiskered catfish, *Sperata aor* (Hamilton, 1822), from the Ganga River; furthermore, the otolith chemistry showed comparatively low temporal variations as compared to spatial variations thereby the classification success (overall correct classification was 83.5%) remained constant over the three selected sampling years (2013, 2014, and

2015). The elements such as Ba, Sr, K, and Mg were used to correctly classify the individuals to their original location of *S. aor* from the Ganga River. The otolith chemistry, truss morphometry of the fish body, and microsatellite markers showed non-significant variation in percentage classification accuracy of *S. aor* stocks from the Ganga River (Nazir 2018). However, these methods showed three to four stocks among the selected locations across the Ganga River (cf. Nazir and Khan 2017; Khan and Nazir 2019; Nazir and Khan 2019).

The majority of the stock discrimination studies using otolith chemistry have not considered the effects of multiple environmental and biological factors that govern the incorporation of elements in otoliths. Therefore, future studies at spatial and temporal scales to disentangle the relative influence of these factors should be undertaken to strengthen our understanding of otolith chemistry and its field applications. Moreover, studies based on otolith chemistry (about 83%) have not described the applications of otolith chemistry for fisheries management (Carlson et al. 2017) because of several limitations mostly in adult fishes such as brief residence time (spawning migration) and slow growth in older fish (Pracheil et al. 2014). Carlson et al. (2017) suggested that the information gap can be filled through descriptive case studies (e.g., identifying natal origins and stock assignment, larval dispersal and population connectivity, stock enhancement, etc.) that elucidate management applications of otolith chemistry both in freshwater and marine ecosystems. Pracheil et al. (2014) suggested that the information produced by otolith chemistry can be used in fisheries management when integrated with other methods (genetics, telemetry, and/or tagging). The otolith chemistry provides information on fish stock structure, life-history, and habitat use which are very useful for fisheries management and conservation thereby fisheries managers can use this method to develop science-based management plans (Pracheil et al. 2014; Tanner et al. 2016; Carlson et al. 2017).

Otolith shape

Otolith shape variation has become widely used for stock discrimination (Burke et al. 2008; Aguera and Brophy 2011; Ider et al. 2017; Moreira et al. 2019) and has advanced from simple distance measurements to geometric morphometry with the improvements in image analyzing tools (Cadrin and Friedland 1999; Stransky 2014). The otolith shape and its utility in stock discrimination have appeared in almost 801 peer-reviewed papers from 2000 to 2019 (Web of Science™, search on 17 September 2020; search term: otolith shape OR otolith morphometry (black bar), and otolith shape OR otolith morphometry AND stock discrimination OR stock delineation OR stock deciphering (grey bar)) (Fig. 2). Otolith morphometry is preferred over the traditional method of morphometric and meristic characters of the fish body because otoliths are usually not affected by the short-term changes in fish
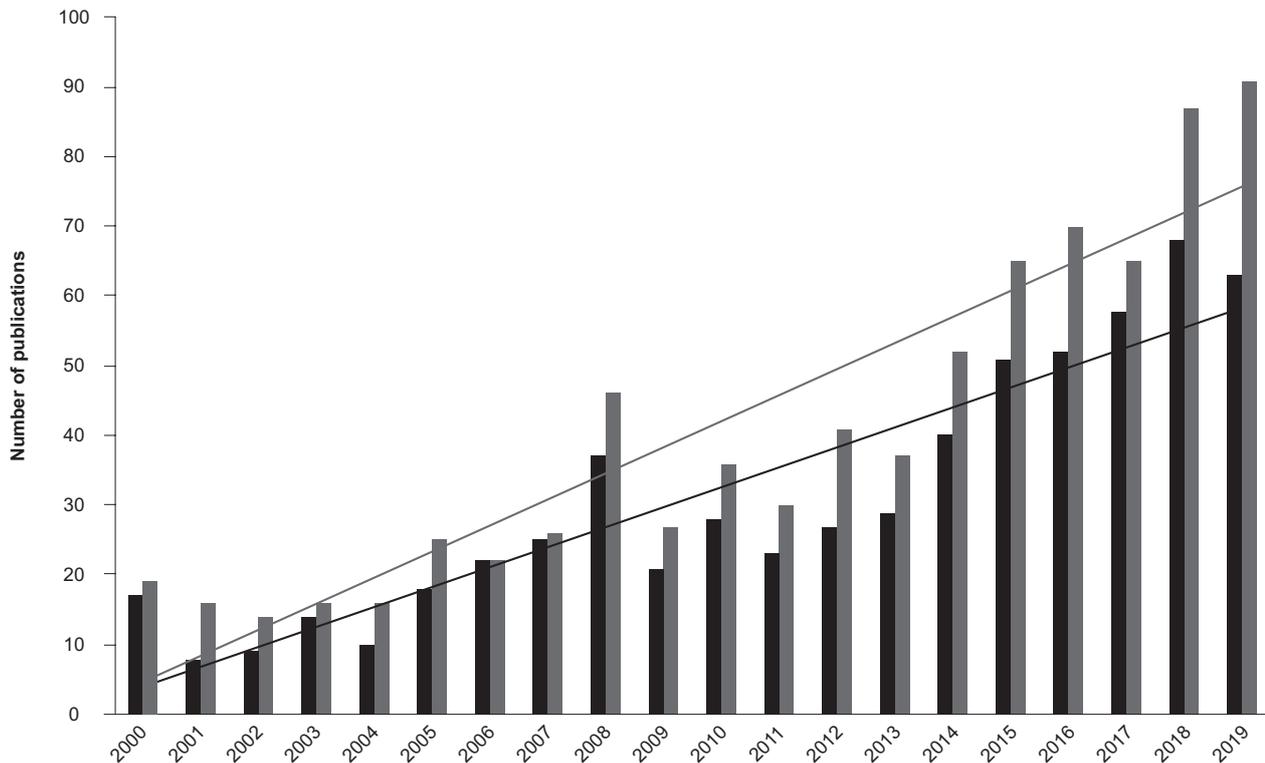
Figure 2. Number of publications per year featuring otolith shape (Web of Science, search on 17 September 2020, search term: otolith shape OR otolith morphometry (black bar), and otolith shape OR otolith morphometry AND stock discrimination OR stock delineation OR stock deciphering (grey bar)). Lines indicate the trends and results were not cross-checked.

condition or preservation of samples (Campana and Casselman 1993). Geometric outline and landmark methods are commonly used to study otolith shape variations between or among fish groups by removing size-dependent variation using an allometric approach (Stransky 2014). Otolith shape variation analysis by geometric outline method involves capturing otolith outline and deriving Cartesian coordinates (*x*, *y*) using image analysis software such as ImageJ (http://rsbweb.nih.gov/ij/) and tps-DIG (http://life.bio.sunysb.edu/morph/) (Stransky 2014). Several methods are being used for fitting outlines; however, the Fourier analysis (FA) is most commonly employed (Stransky 2014) but has limited applicability for otoliths which show significant and complex curvatures. The issues with Fourier analysis can be alleviated by using Elliptical Fourier analysis (EFA) which decomposes the complex curves of otoliths by generating the sum of harmonically related ellipses (Crampton 1995; Tracey et al. 2006; Stransky 2014). The Wavelet transform can be used as a substitute to the usually applied Fourier transform. Moreover, the Wavelet transform can resolve the problem of poor estimation of sharp edges of otoliths associated with Fourier transform (Libungan and Palsson 2015). The software products for FA of 2D outlines are HANGLE, HMATCH, and HCURVE (Crampton and Haines 1996) while for EFA, EFAwin (Isaev and Denisova 1995), SHAPE package (Iwata and Ukai 2002), and ShapeR and Momocs packages in the R environment (Libungan and Palsson 2015; Brophy et al. 2016; Denechaud

et al. 2020) are commonly used. The ShapeR package is more common as it has been specifically designed for otolith shape study while Momocs on the other hand is used for general image and shape analysis.

Otolith shape analysis has been used for stock discrimination in a number of fish species. For example, Aguera and Brophy (2011) reported that the Atlantic saury, *Scomberesox saurus saurus* (Walbaum, 1792), larvae exposed to different ambient conditions in the Mediterranean Sea and the North-eastern Atlantic and irrespective of where they have spawned show distinct stocks with a cross-validated correct classification of 86%. Moreover, the Mediterranean and Atlantic show considerable difference in environmental factors, such as temperature, salinity, and food availability (Patarnello et al. 2007) which could have affected the growth rates of the fish that exist there and may be responsible for significant changes in fish condition between saury from these two regions. The stock structure of Atlantic saury is still unclear because of limited studies and therefore, this species should be managed like other short-lived forage species (Aguera and Brophy 2012). Paul et al. (2013) described that the two stocks of cod, *Gadus morhua*, in the Baltic Sea show significantly different otolith shape and more than 90% of the individuals were correctly classified to one of the two stocks. These findings highlight that the otolith shape analysis can be effectively used to discriminate adults of Baltic cod stocks. Similarly, two genetic stocks of Baltic cod with a classification accuracy of

92% were reported but these two stocks show considerable mixing, thereby future studies should evaluate the mixing dynamics of populations to fully understand the ecology of the species (Weist et al. 2019). Keating et al. (2014) stated that the blue whiting, *Micromesistius poutassou* (Risso, 1827), population in the North-eastern Atlantic was classified into two morphotypes (99% correct classification success) with a strong latitudinal influence despite the complex stock structuring at the spawning grounds. Furthermore, consistent with earlier studies of stock differentiation in blue whiting, the results further suggested the blue whiting to be considered as separate stocks because of separate feeding and breeding grounds with varying degree of mixing in the common spawning grounds. Previous studies have reported some degree of genetic differentiation among blue whiting spawning groups, however, these differences reflect only a snapshot in time and there are enough chances of intermixing of populations at the breeding grounds (Mork and Giaever 1995; Was et al. 2006). Vasconcelos et al. (2018) studied the population structure of blue jack mackerel, *Trachurus picturatus* (Bowdich, 1825), in the North-eastern Atlantic (Peniche, Madeira, and Canary islands) using otolith shape and they found three populations with an overall 73.3% correct classification. Further, the authors reported that the remaining percentage represents misclassification which may be due to the migration driven by feeding and spawning requirements. The use of parasites as a tag revealed the presence of three stocks (Portuguese mainland, Madeira archipelago, and Canary archipelago) of blue jack mackerel in the North-eastern Atlantic (Vasconcelos et al. 2017). In another study on the blue jack mackerel,

four stocks namely Portugal mainland, Azores, Madeira, and the Canaries were identified from North-eastern Atlantic with an overall classification success of 81% using otolith microchemistry (Moreira et al. 2018).

During the review of literature, the interest in population discrimination was much lower in freshwater ecosystems where exploitation is less in scale and populations are often well spatially-separated compared to marine ecosystems. In general, the otolith shape method itself is not comparably less used but there are simply fewer analyses of population discrimination in freshwater ecosystems. The utility of otolith shape for stock discrimination has shown an increasing trend because it can be used as a complementary technique that certainly can improve our understanding of the stock structure (Begg and Waldman 1999; Cadrin 2000; Begg et al. 2005; Campana 2005). Further, it is a less expensive tool as compared to genetic markers or otolith chemistry.

Otolith chemistry and otolith shape: a complementary approach

In the past two decades, the number of publications per year based on otolith chemistry and otolith shape is showing an increasing trend (Web of Science™, search on 17 September 2020, search term: otolith chemistry OR otolith microchemistry OR otolith elemental composition (black bar), otolith shape OR otolith morphometry (grey bar), and otolith chemistry OR otolith microchemistry OR otolith elemental composition AND otolith shape OR otolith morphometry (light grey bar)) (Fig. 3). Several studies
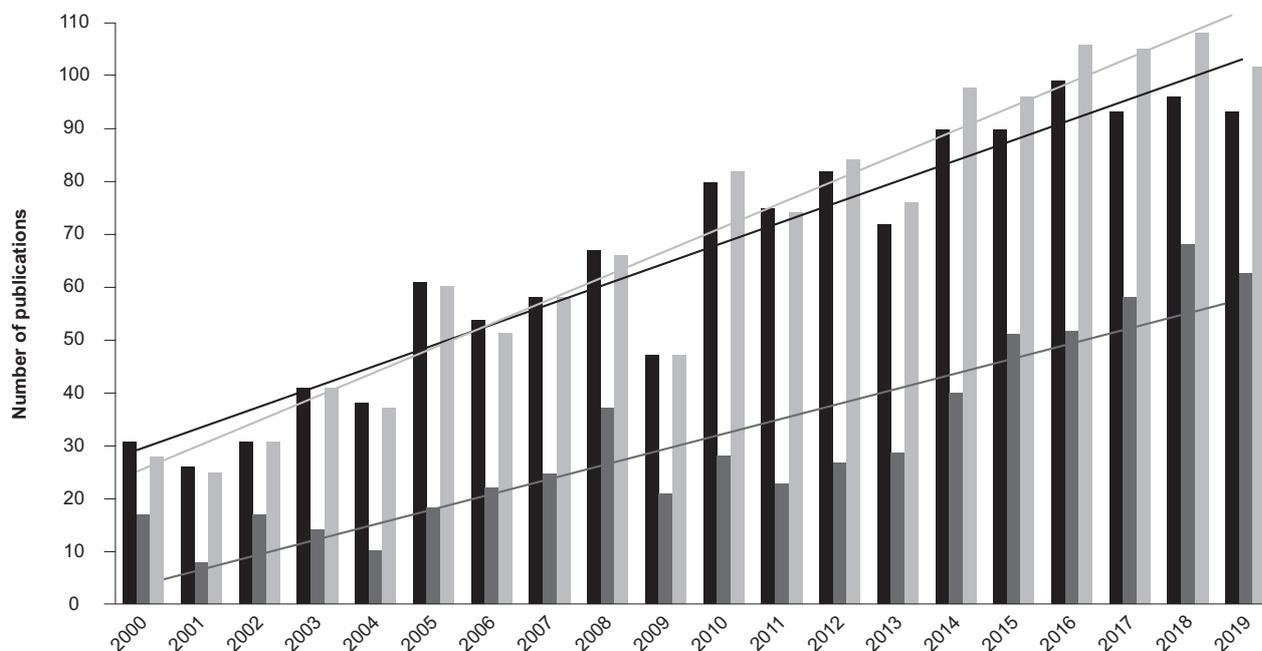

Figure 3. Number of publications per year featuring otolith chemistry and otolith shape (Web of Science, search on 17 September 2020, search term: otolith chemistry OR otolith microchemistry OR otolith elemental composition (black bar), otolith shape OR otolith morphometry (grey bar), and otolith chemistry OR otolith microchemistry OR otolith elemental composition AND otolith shape OR otolith morphometry (light grey bar)). Lines indicate the trends and results were not cross-checked.

have reported that the otolith chemistry and shape provide concordance in results but some workers have argued that otolith chemistry is more efficient in discriminating fish stocks (Turan 2006; Longmore et al. 2010; Ferguson et al. 2011). Turan (2006) demonstrated that the otolith shape and chemistry can be used as complementary techniques and both these methods showed two stocks (the central Black Sea and Aegean Sea stocks) of the Mediterranean horse mackerel, *Trachurus mediterraneus* (Steindachner, 1868). However, no stock separation was found in a previous study based on morphometric and meristic data (Turan 2004). Turan (2006) also found no significant correlation between geographical distances with the Euclidean distances for both the selected methods thereby showing that the geographic distance does not restrict the movement of *T. mediterraneus* populations among selected areas. Moreover, the otolith shape revealed 79% while otolith chemistry showed 83% correct classification thereby the individuals of this species may have spent a significant part of their lives in different environmental conditions. Longmore et al. (2010) examined spatial variations in a deep-sea teleost, *Coryphaenoides rupestris* Gunnerus, 1765, collected from different areas in the North Atlantic using otolith chemistry and shape. Overall, otolith chemistry (92% classification success) was comparatively more successful in identifying individual fish from different areas as compared to otolith shape (43% classification success). The high percentage of correct classification obtained using otolith chemistry showed that the individual fish inhabiting different deep sea areas can be accurately delineated to their original stock. The otolith shape showed low classification accuracy (<50%) and similar results were found in another deep sea fish, the beaked redfish, *Sebastes mentella* Travin, 1951 (see Stransky 2005). The strong variations in classification accuracy between otolith chemistry and shape in deep sea fishes may be because of slow growth and deep sea do not show strong variations in environmental conditions (Longmore et al. 2010). The authors also recommended further studies to evaluate the extent of otolith chemistry reflect actual stock structure by investigating chemical signatures across different life history events and to compare the results with genetic data. In another study, a similar approach was used to discriminate stocks of mulloway, *Argyrosomus japonicus*, collected from western, central, and eastern coasts of South Australia (Ferguson et al. 2011). The stock discrimination methods provided complementary results although allocation success was lower for otolith shape and morphometric indices (83%) compared to the elemental composition of the otolith edge (94%). Although, the otolith shape and morphometric indices showed that the regional differences were temporally stable but the authors recommended the comparison of otolith shape between sexes, size-classes, and multiple spatial and temporal scales to understand the potential utility of this method in stock discrimination. Barnes et al. (2016) investigated the genetic stock structure of mulloway, *A. japonicus*, within Australian waters and between Australia and South Africa, and reported strong genetic variations between Australia and South Africa using microsatellite markers. Izzo et al. (2017) studied age-related and temporal patterns of the stock structure of sardine, *Sardinops sagax* (Jenyns, 1842), collected from South Australia and the east coast through combined analysis of otolith chemistry and shape using archived otoliths. The integrated analysis of otolith chemistry and shape revealed the presence of separate stocks of young sardine (1–3 years of age) in northern and southern New South Wales. However, the occurrence of age-related and temporal patterns of stock sub-structuring of sardine in Australian waters complicates the separation of discrete stocks (Izzo et al. 2017). Soeth et al. (2019) studied the stock structure of Atlantic spadefish, *Chaetodipterus faber* (Broussonet, 1782), from the South-western Atlantic Ocean and found spatially structured semi-discrete groups between 23°S and 27°S with the possibility of intermixing. The authors further suggested that the local populations of *C. faber* should be considered as different stocks even with the possibility of an intermingling of populations and without knowing the recruitment sources in the Brazilian South-western Atlantic coast. Further, the overall classification success was 59% and 76% as shown by otolith shape and chemistry, respectively. However, when the authors combined the data of both the techniques the overall classification success increased to 83%. Therefore, the concurrent use of otolith chemistry and shape is desirable to maximize the likelihood of correct classification of individuals to their original populations. Machado et al. (2017) reported tropical and subtropical clades of *C. faber* based on mitochondrial DNA and haplotype distribution showed peripheral isolation throughout Southwestern Atlantic between 2°S and 27°S.

The choice of stock discrimination methods is important because each method has its particular associated challenges such as ecological interpretation, spatio-temporal variations, discriminatory power, and related expenses (Tanner et al. 2016). Therefore, the comparison of methods is recommended because sometimes a single method may fail to identify stock separation. During the review of different studies, we found that a single method may not show stock discrimination because of several reasons such as the fish population is homogeneous especially in the marine environment, the marker may fail to detect changes at spatial and temporal scales, and the discrimination power of the method is very low. Therefore, two or more methods should be used complementarily to study the stock structure, and connectivity of fish populations at common breeding and feeding grounds (Randon et al. 2020). The concurrent use of several stock discrimination techniques operating over broader spatial and temporal scales may provide sufficient data to understand both evolutionary and ecological processes that sustain the fish stock structure (Abaunza et al. 2008; Taillebois et al. 2017). The holistic approaches combining otolith chemistry with different and potentially complementary tools may explicitly determine the stock structure and promote interconnection between management

plans and biological processes (Welch et al. 2015; Tanner et al. 2016). Further, to investigate the utility of otolith chemistry and shape for stock discrimination, the genetic markers especially microsatellite markers or single nucleotide polymorphism (SNPs) should be used to complement the information of stock structure (Ferguson et al. 2011; Soeth et al. 2019). Currently, there is a need to develop new technology, statistics, and/or integrate methods to define the stocks and to include the information of population structure into fisheries management especially when there is a mismatch between population structure and management units (Kerr et al. 2017).

Otolith chemistry in association with growth increments can be used to document the environment information in which fish species live and habitat changes throughout ontogeny (Sturrock et al. 2012; Tanner et al. 2016). Further, the otolith chemistry provides complete information on fish migration which makes it unique when compared with other available tools (Secor 2010). Generally, the otolith chemistry studies have provided ample information on several processes such as natal origin, connectivity, migration pattern, life history events, spawning and nursery areas, etc. with cost-effective methodologies (Avigliano and Volpedo 2016). The seasonal pattern of trace elemental incorporation in otoliths is being used as a tool for age estimation and validation in the fish species which do not show significant contrast between growth bands (Hussy et al. 2016b; Heimbrand et al. 2020). However, more studies are warranted to validate this technique particularly if annual changes in fish growth rate do not occur. Currently, otolith chemistry has been used as an intrinsic proxy of fish metabolism to understand how a species interact with their environment to survive but it is very challenging to study in natural conditions (Chung et al. 2019; Martino et al. 2020).

Conclusion

In recent years, the information contained within otolith chemistry and shape has been commonly used for fish stock discrimination and to interlink management strategies and biological processes. However, the otolith chemistry and shape are influenced by several exogenous and endogenous factors. Several studies have reported that temperature and salinity are important environmental factors influencing otolith chemistry but these studies usually have not utilized a broad range of temperature and salinity typically the fish experience in nature. Comprehensive in situ validation experiments across a complete reproductive cycle should be undertaken to fully understand the relation between these factors and the otolith chemistry. The biokinetic and bioenergetics models can be used to evaluate a suite of environmental and biological factors influencing the uptake of elements in otoliths. The relation between calcium polymorphs and the rate of elemental uptake needs further assessment. To fully utilize otolith chemistry for stock discrimination at both spatial and temporal scales, it is recommended to build a multi-year database of otolith chemistry and water chemistry signatures. The complete understanding of local environmental conditions and genetic factors influencing otolith shape requires further investigations. The introduction of exotic fish species having distinct evolutionary histories can provide an effective method to analyse the influence of environment and genetics on otolith shape. A complementary approach is desirable because of the limitations and assumptions associated with any particular method and as far as proper fisheries management is concerned. Further, a collaboration between different stakeholders should be mediated by fisheries managers about the utility of otolith chemistry and shape to bridge the gap between research and ecosystem-based fisheries management.

Acknowledgments

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