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## Review: Linking physiology and biomineralization processes to ecological inferences on the life history of fishes

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### ABSTRACT

Biomineral chemistry is frequently used to infer life history events and habitat use in fishes; however, significant gaps remain in our understanding of the underlying mechanisms. Here we have taken a multidisciplinary approach to review the current understanding of element incorporation into biomineralized structures in fishes. Biominerals are primarily composed of calcium-based derivatives such as calcium carbonate found in otoliths and calcium phosphates found in scales, fins and bones. By focusing on non-essential life elements (strontium and barium) and essential life elements (calcium, zinc and magnesium), we attempt to connect several fields of study to synergise how physiology may influence biomineralization and subsequent inference of life history. Data provided in this review indicate that the presence of non-essential elements in biominerals of fish is driven primarily by hypo- and hyper-calcemic environmental conditions. The uptake kinetics between environmental calcium and its competing mimics define what is ultimately incorporated in the biomineral structure. Conversely, circannual hormonally driven variations likely influence essential life elements like zinc that are known to associate with enzyme function. Environmental temperature and pH as well as uptake kinetics for strontium and barium isotopes demonstrate the role of mass fractionation in isotope selection for uptake into fish bony structures. In consideration of calcium mobilisation, the action of osteoclast-like cells on calcium phosphates of scales, fins and bones likely plays a role in fractionation along with transport kinetics. Additional investigations into calcium mobilisation are warranted to understand differing views of strontium, and barium isotope fractionation between calcium phosphates and calcium carbonate structures in fishes.

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### 1. Introduction

In the present day, the fisheries biology research community directly applies biomineralized structure microchemistry to habitat and life history determination particularly for freshwater to saline water movements (Campana, 1999). Although there is much success in these applications, limitations also exist suggesting insufficient understanding of element presence in biominerals (Sturrock et al., 2012, 2014). Initial examination of how each structure is formed on a biogeochemical level provides the basic understanding of hard structure biomineralization (Bäuerlein et al., 2007; Mann, 2001). Calcium carbonate and calcium phosphate hard structures have different chemical properties and affinities for element substitution and insertion in association to the protein matrix during the biomineralization process (Bäuerlein et al., 2007; Doubleday et al., 2014; De Pontual and Geffen, 2002;

Mann, 2001). The building block for all these structures involves calcium, and its mobilisation and remobilisation within a fish (Allemand et al., 2008; Mann, 2001; Schönböner et al., 1979; Weiss and Watabe, 1979). Element presence within hard structures can be viewed in terms of essential and non-essential need for life (Crichton, 2008). This qualification plays a large role in the function of the element once available internally to an organism and before incorporation and measurement in biominerals (Crichton, 2008). Physiologically, an organism can then control the presence of elements particularly divalent cations either indirectly through calcium uptake mechanisms for non-essential elements or directly for essential life elements (Bijvelds et al., 1998; Chowdhury and Blust, 2011; Eide, 2006; Feng, 2011; Lee et al., 2015; Mann, 2001; Nachshen and Blaustein, 1982; Omelon et al., 2009; Swenson et al., 2014; Van Campenhout et al., 2009; Wang and Berlin, 2007; Zhou and Clapham, 2009). This further leads to isotopic discrimination based on energetics in uptake pathways (Kedem and Essig, 1965; Sharp, 2007). By bringing the research fields of fisheries biology, biogeochemistry, and physiology together, a new perspective to the current state of element applications to biomineralized structures

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is highlighted suggesting a multi-disciplinary approach to the research questions in this field.

Living organisms selectively extract and take up elements from their environment and incorporate them into tightly controlled functional biological structures. These biologically derived minerals (biominerals) act as protective structures, aid in movement, feeding, buoyancy, vision, gravity sensing and sound detection, and allow for storage of key elements (Bäuerlein et al., 2007; Mann, 2001). Of particular relevance to this review is the storage of ~99% of the whole-body fraction of calcium ( $\text{Ca}^{2+}$ ) in biomineralized structures such as otoliths, scales, fins and bones within a teleost (Flik et al., 1986).

Calcium is a fundamental element forming the foundation of biominerals, as well as being essential for other physiological functions such as muscle fibre contraction, intracellular messaging, and reproduction (Crichton, 2008). As a consequence calcium concentration in both intracellular and extracellular fluid environments is tightly controlled at the level of the cell and whole body so that normal physiological function can be maintained (Bijvelds et al., 1995; Flik et al., 1984, 1995, 1996).

In teleost fish, homeostatic regulation of calcium is a primary function of the gill (Flik and Verbost, 1993; Herrmann-Erlee and Flik, 1989; Perry et al., 1992), and secondarily the intestinal epithelia (Flik and Verbost, 1993; Wilson and Grosell, 2003) with the opercular epithelia playing a minor role (Marshall et al., 1992; McCormick et al., 1992). Within the gills, mitochondrial rich cells (MRC) or ionoregulatory cells and pavement or respiratory cells, have both been shown to be involved in calcium uptake (Flik et al., 1995). Evidence in some fish species of gastrointestinal uptake is observed (Allen et al., 2011; Flik et al., 1990; Flik and Verbost, 1993; Genz et al., 2013), for example in Atlantic cod (*Gadus morhua*), intestinal calcium uptake was estimated at 30% of the total uptake (Sundell and Björnsson, 1988). Although the renal system is not recognised as an uptake mechanism from the environment, it does play a role in internal calcium homeostasis by excreting excess ions when necessary, such as periods of high environmental calcium (e.g., seawater environment) and/or increased dietary calcium intake (Flik et al., 1996).

Calcium is stored in organisms in the form of calcium carbonate ( $\text{CaCO}_3$ ) and hydroxyapatite ( $\text{Ca}_5(\text{PO}_4)_3(\text{OH})$ ). Calcium carbonate found within the hearing systems of mammals and fish (otoconia in mammals analogous to otoliths in fish) is a calcium sink due to the lack of resorbable qualities of the structure once formed (Allemand et al., 2008). Conversely, bone-like structures (bones, fins, scales) can be reabsorbed which results in a remobilisation of calcium in the ionic form –  $\text{Ca}^{2+}$ . One well-documented mode for the reabsorption of calcium from bone in mammals is through the dissolution of bone stores by osteoclasts (Schönbömer et al., 1979; Weiss and Watabe, 1979).

In the following review we focus on teleost and chondrostei fish in particular and examine the incorporation of strontium, barium, magnesium and zinc into biominerals. Each of these elements shares a commonality in that they are all, like calcium, divalent cations in solution (Allemand et al., 2008; Campana, 1999; De Pontual and Geffen, 2002). Strontium and barium are non-essential and typically considered trace elements that substitute directly for calcium in biomineralization of the crystalline inorganic structure (Allemand et al., 2008; Campana, 1999; De Pontual and Geffen, 2002; Doubleday et al., 2014) and have been extensively used to infer various life history, habitat, chemical marking and biological characteristics of freshwater and marine fishes (Campana, 1999; Brown and Severin, 2009; Elsdon and Gillanders, 2003, 2006; Elsdon et al., 2008). Magnesium (bulk element) and zinc (trace dietary requirement) are essential elements also used to infer life history traits, but are more likely to be incorporated in the protein organic compartment of the biomineral in otoliths although magnesium can also be directly substituted for calcium in hydroxyapatite mineralisation (Crichton, 2008; Mann, 2001; Omelon et al., 2009). Given the different end fates of these two groups of substituting elements in biominerals, strontium and barium are expected to be

governed principally by regulatory drivers of calcium (Mann, 2001), whereas, the magnesium and zinc concentrations are governed by their own regulatory processes (Crichton, 2008). When all these elements are considered together, stronger inferences regarding physiological mechanisms of element incorporation into biomineralized structures can be made.

### 1.1. Microchemistry of calcium-based hard structures

To date the most extensive knowledge base regarding hard structure microchemical and isotope analyses is the identification of habitat switching in teleosts (Campana, 1999, 2005; Elsdon et al., 2008; Gillanders, 2005; Kennedy et al., 2000; Muhlfeld et al., 2012). Anadromy (i.e., the movement of fish between fresh and marine waters) is often inferred by otolith strontium/calcium ratios because otolith and environmental strontium/calcium ratios tend to be positively correlated and elevated in marine compared to freshwater environments (Brown and Severin, 2009). Specific studies on a number of salmonids, White Sturgeon (*Acipenser transmontanus*), and Green Sturgeon (*Acipenser medirostris*) have reported movement of individuals from freshwater habitats into marine or coastal waters through otolith or fin ray element analyses (Allen et al., 2009; Veinott et al., 1999; Zimmerman, 2005).

Examination of otolith strontium isotopic ratios of fishes confined within freshwater systems has also allowed for inference of patterns of habitat switching at micro-scales within watersheds. The success of these techniques is highlighted by studies on Atlantic Salmon (*Salmo salar*) in tributaries of the Connecticut River (Kennedy et al., 2000, 2002), Chinook Salmon (*Oncorhynchus tshawytscha*) in the California Central Valley (Barnett-Johnson et al., 2008), Cutthroat Trout (*Oncorhynchus clarki*) in the Flathead River drainage of the Rocky Mountains (Muhlfeld et al., 2012), and for Chinook Salmon within Bristol Bay, Alaska (Brennan et al., 2015b). Groundwater hydrology and underlying geological conditions are instrumental in determining local environmental strontium isotopic ratios that are reflected in otolith composition (Brennan et al., 2014, 2015a, 2015b; Hegg et al., 2013). However, this approach is inappropriate in purely marine fishes where the isotopic ratio of environmental strontium ( $^{86}\text{Sr}/^{87}\text{Sr}$  of  $0.70918 \pm 0.00006$ ) is constant due to long residence times of strontium and relatively short turnover rate of the world's oceans (Faure and Mensing, 2005).

In marine systems, migrations between coastal areas or marine habitats are sometimes observed although otolith and environmental concentrations of strontium in these systems are more complex. Campana et al. (1994) and Tanner et al. (2013) demonstrated differential habitat use during life history of Atlantic cod and Common Sole (*Solea solea*) for marine and tidal estuary regions, respectively but a multiple element analysis was needed as increased difficulty was observed in linking otolith microchemistry to individual water masses within the study area. Further, examination of multiple freshwater, anadromous and marine species ( $n = 81$ ) concluded that environmental strontium/calcium drives otolith strontium/calcium in anadromous and freshwater species but not in marine species (Brown and Severin, 2009).

In recent years, microchemical and isotopic analysis of biominerals has been frequently used in biological research (>1900 primary articles published based on the search criteria in Google scholar linked to the University of Manitoba's library databases of "fish" and "otolith" or "fin" or "scale" and "microchemistry" or "trace element" or "isotope"). Despite this large body of primary literature, a lack of complete understanding between the connectivity of fish physiological control mechanisms and the presence of elements in biominerals is evident (Sturrock et al., 2012, 2014). While most deviations from the expected relationship between otolith and environmental strontium/calcium have been reported for marine species (Brown and Severin, 2009; Sturrock et al., 2012, 2014), there are also instances in freshwater systems. For example, we have observed strontium profiles (Fig. 1) that suggest lake-dwelling Arctic Char, (*Salvelinus alpinus*), are migrating between marine

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