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Effects of water temperature and barium concentration on otolith composition along a salinity gradient: Implications for migratory reconstructions

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ABSTRACT

Analysis of naturally occurring variation in otolith elemental composition has become a common approach for retrospectively determining migratory history in diadromous fishes. Environmental factors, such as temperature, salinity, and ambient water concentration, can independently, or in an interactive manner, affect elemental incorporation rates. Furthermore, the relative importance of kinetic and metabolic (or "vital") effects on elemental incorporation remains unclear. In this study, a repeated measures design was used to: (1) quantify the effects of water temperature (9 °C, 12 °C, 15 °C) and freshwater Ba:Ca levels (low, intermediate, and high) on elemental partitioning and otolith composition (Mg:Ca, Sr:Ca, Ba:Ca) in juvenile Chinook salmon (*Oncorhynchus tshawytscha*) along a salinity gradient (0, 5, 10, 14); and (2) estimate the lag time between physical exposure to chemically distinct water masses and changes in otolith composition. Additionally, relationships between elemental incorporation and somatic and otolith growth rates were evaluated across and within temperature treatments to identify potential rate effects. Otolith incorporation of Sr and Ba was positively related to water concentration whereas Mg incorporation was not. For Sr and Mg, there were significant interactions between temperature and salinity ($p \leq 0.01$). For Ba, there were complex interactions among temperature, water Ba:Ca values, and salinity ($p \leq 0.01$). In certain instances, interactive effects of temperature and salinity were large enough to confound interpretation of field data. Furthermore, there was evidence for negative effects of somatic growth rate on the incorporation of Ba that were consistent across temperatures ($r = -0.32$ to -0.72). Observations were consistently contrary to expectations based on models of elemental incorporation for abiotic aragonite, highlighting the importance of vital effects and indicating that species-specific models of incorporation may be necessary. Changes in otolith composition were detected within 2–3 d of a change in water composition but otolith composition did not stabilize for 12–14 d, indicating that habitat transitions should be discernable in a short period of time but the otolith may not reflect ambient water levels for up to 2 weeks. These observations underscore the need to evaluate the effects of abiotic and biotic factors on otolith elemental incorporation in settings that mimic natural conditions to accurately interpret field data.

1. Introduction

Examination of natural and artificial intrinsic (Secor et al., 2001; Swearer et al., 2002; Taylor and Hellberg, 2003) and extrinsic (Block et al., 2001; Rooker et al., 2008; Skomal et al., 2009) markers has advanced our understanding of dispersal and movement patterns in fishes. In particular, variation in otolith elemental composition has been used frequently to reconstruct migratory history in diadromous fishes (reviewed in Elsdon et al., 2008). Certain divalent cations, such as Sr^{2+}, occur in biogenic carbonates in proportion to their environmental variability and, thus serve as environmental proxies. For example, threshold levels of otolith strontium:calcium (Sr:Ca) indicative of residence in fresh, brackish, or oceanic waters are commonly established based on fish collected in representative environments (Daverat et al., 2006; Thibault et al., 2007; Zlokovitz et al., 2003). Alternatively, laboratory experiments have been undertaken to determine species-specific relationships between water and otolith Sr:Ca and evaluate the effects of environmental variables, such as temperature and ambient water concentration, prior to field application (Elsdon and Gillanders, 2002; Limburg, 1995; Secor et al., 1995). However, few laboratory studies simulate a suite of natural conditions during diadromous migration and evaluate the potential to misinterpret field-derived otolith data.

Otolith Sr:Ca is most commonly used to reconstruct diadromous migrations; however, water Sr:Ca displays minimal variation above salinities of ~8–10 (Kraus and Secor, 2004; Zimmerman, 2005). Therefore, researchers have explored other markers, including Ba:Ca, Li:Ca, $\delta^{13}C$ and $\delta^{18}O$ (Arai and Hirata, 2006; Elsdon and Gillanders, 2005a; Hicks et al., 2010) to differentiate among freshwater, estuarine, and ocean residences. The successful application of any of

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these markers requires knowledge of their spatial and temporal distributions in the environment as well as an understanding of the mechanisms regulating otolith elemental incorporation. Although both kinetic and metabolic (or "vital") effects can influence elemental incorporation in biogenic carbonates (Campana, 1999; Gaetani and Cohen, 2006; Morse and Bender, 1990), specific regulatory processes driving observed variation have yet to be elucidated. Given the clear presence of species-specific vital effects on otolith elemental incorporation (Melancon et al., 2009), the development of a widely applicable model of incorporation based on "first principles" in the near future appears unlikely. It may be necessary to examine multiple tracers and/or develop species-specific models of incorporation to provide the appropriate framework for field applications.

Chinook salmon (*Oncorhynchus tshawytscha*) is an anadromous species with a diverse life history. The size and timing of juvenile entry into the marine environment are considered important factors in survival (Scheuerell et al., 2009; Waples et al., 2007; Zabel and Achord, 2004). It is hypothesized that subsequent survival is related to the timing of marine entry in relation to production of available prey, i.e., the match–mismatch hypothesis (Cushing, 1975; 1990), and that survival is positively related to size upon marine entry, i.e., the bigger-is-better hypothesis (Anderson, 1988; Litvak and Leggett, 1992; Sogard, 1997). These hypotheses can be directly evaluated using otolith structural and chemical analyses to generate robust, quantitative estimates of the size and timing of marine entry for individuals collected at any age. However, a more thorough understanding of how environmental factors, such as temperature, water concentration, somatic growth rate, and otolith precipitation rate, influence elemental incorporation is needed (Elsdon et al., 2008). Additionally, previous researchers have demonstrated that there can be significant lags ($\geq$15 d) between changes in water chemistry and subsequent change in otolith composition (Elsdon and Gillanders, 2005b; Lowe et al., 2009; Macdonald and Crook, 2010). Therefore, it is also critical to determine how rapidly otolith composition changes in response to variation in water composition.

In many coastal systems, Sr and Ba water concentrations are inversely related, with higher Sr and lower Ba concentrations in marine compared with fresh waters. Therefore, researchers have explored the potential of combining otolith Sr:Ca and Ba:Ca to improve migratory reconstructions of diadromous species (Elsdon and Gillanders, 2005a; Hamer et al., 2006; McCulloch et al., 2005). Variation in temperature, salinity, and freshwater Sr and Ba concentrations may independently, or in an interactive manner, alter incorporation rates, potentially confounding otolith interpretations. Therefore, I used a repeated measures design to: (1) evaluate the effects of water temperature (9 °C, 12 °C, 15 °C) and freshwater Ba:Ca levels (low, intermediate, and high) on elemental partitioning (Mg, Sr, Ba) and otolith composition in juvenile Chinook salmon across salinities (0, 5, 10, 14); and (2) estimate the time required for otolith composition to change after physical exposure to chemically distinct water masses. In addition to Sr and Ba, Mg was included because water Mg:Ca varies with salinity and otolith Mg:Ca displays extensive variation among groups of marine (Campana et al., 2000; Thorrold et al., 1998; Thresher, 1999), euryhaline (Miller, 2007), anadromous (Arai and Hirata, 2006) and freshwater fishes (Veinott and Porter, 2005; Wells et al., 2003). However, controlled laboratory experiments have generated equivocal results regarding the effects of water Mg:Ca, temperature, and growth rate on otolith incorporation of Mg (Elsdon and Gillanders, 2002; Fowler et al., 1995; Martin and Thorrold, 2005). Finally, potential effects of somatic and otolith growth rate on elemental incorporation were evaluated across and within temperature treatments.

2. Methods

2.1. Experimental conditions

Juvenile Chinook salmon were collected from the Salmon River Hatchery in Otis, Oregon on 01 May 2008. Fish were acclimated to laboratory conditions (12L:12D, 12 °C) for 7 d, after which water temperature was dropped by 5 °C for 24 h to establish a visual check on the otoliths (Volk et al., 1984). This check, in conjunction with daily otolith increment analysis (Neilson and Geen, 1982), was subsequently used to identify the beginning of the experiment. A subset of individuals ($n=25$) was weighed (nearest 0.01 g) and measured (0.5 mm). Fifteen fish were then placed in each of 27 15-L tanks. Fish were haphazardly assigned to a tank, and tanks were randomly distributed within temperature-controlled, flow-through water baths. Treatments included three water temperatures (9 °C, 12 °C, 15 °C) and three freshwater Ba:Ca levels (low, intermediate, high). All temperature × freshwater Ba:Ca treatment combinations were then exposed sequentially to four salinities (0, 5, 10, 14) (described further below).

Temperature and freshwater Ba:Ca treatments were applied throughout the entire experiment (62 d) whereas salinity was gradually increased over time, simulating natural migration patterns. Ba:Ca treatments were selected to represent emigration from rivers with low (220 μmol mol^{-1}), intermediate (525 μmol mol^{-1}), and high (1035 μmol mol^{-1}) Ba:Ca levels. Fish were initially exposed to one of the Ba:Ca water level × temperature treatments, i.e., low, intermediate, or high freshwater Ba:Ca at 9 °C, 12 °C, or 15 °C. On day 32, seawater was mixed with freshwater to increase salinity to 5 in all tanks. On day 40, salinity was increased to 10 and, after 9 additional days, salinity was increased to 14 for the remaining 13 d of the experiment. On day 62, all fish were euthanized, weighed (0.01 g), measured (0.5 mm), and otoliths removed immediately. Therefore, fish within a treatment remained within a freshwater Ba:Ca treatment (low, intermediate, or high) at a specific temperature throughout the entire experiment yet experienced a gradual increase in salinity from 0 to 14 in the final 31 d of the 62-d experiment. Barium was added to fresh water prior to mixing with salt water to simulate mixing as it would occur in the field; therefore, Ba:Ca water levels mimic natural conditions but were not constant across salinities. Barium treatments were generated by adding BaCl (SPEX Certiprep® Group certified reference materials) to freshwater.

Water temperature, ammonia, and dissolved oxygen levels within each tank were monitored daily. Approximately 50% of the water within each tank was exchanged every 2–3 d. Several batches of water with appropriate barium spikes and salinity were prepared for each treatment during each water exchange. Tanks within a treatment received a mixture of 2 to 3 batches per exchange. Fish were fed to apparent satiation daily with artificial feed (BioOregon®). Artificial feeds are relatively high in marine protein and, thus, relatively high in Sr (1.2–1.7 mmol mol^{-1}) (Gibson-Reinemer et al., 2009; J. Miller, unpublished data). Evidence based on incorporation of $^{87}Sr/^{86}Sr$ indicates that ~30% of the otolith Sr during freshwater residence is derived from food (Kennedy et al., 2002; Miller et al., 2010a,b; Weber et al., 2002). Therefore, in this study, observed otolith Sr:Ca values may be higher than expected based on freshwater Sr:Ca alone. However, given that all experimental fish were fed the same food source, any conclusions regarding relative treatment effects remain valid and informative.

2.2. Water collection and analysis

Water samples for elemental analysis were collected from each tank at approximately weekly intervals during the freshwater rearing phase and once per salinity treatment (5, 10, and 14). Samples were filtered (0.45 μm) and acidified using standard methods (Eaton et al. 2005). Standard calibrations were generated with SPEX Certiprep® Group certified reference materials and Mg, Ca, Sr, and Ba concentrations were measured with a Teledyne Leeman Prodigy inductively coupled plasma-optical emission spectrometer. Samples of known concentration (National Institute of Standards and Technology (NIST) 1643e) were used to estimate accuracy; measured concentrations