

## BRIEF COMMUNICATIONS

### Validation of daily increments and a marine-entry check in the otoliths of sockeye salmon *Oncorhynchus nerka* post-smolts

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Juvenile sockeye salmon *Oncorhynchus nerka* that were reared and smolted in laboratory conditions were found to produce otolith daily increments, as well as a consistently visible marine-entry check formed during their transition to salt water. Field-collected *O. nerka* post-smolts of an equivalent age also displayed visible checks; however, microchemistry estimates of marine-entry date using Sr:Ca ratios differed from visual estimates by c. 9 days suggesting that microstructural and microchemical processes occur on different time scales.

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Calcified structures often produce periodic increments that can be used to estimate age and growth. Otoliths are frequently preferred in these studies as they are formed early in fish development and cannot be resorbed like scales (Campana & Thorrold, 2001). Moreover, periods of physiological stress (e.g. the transition from freshwater to saltwater habitats and first feeding) can cause discontinuities, or checks, in the daily increment sequence characterized by increased opacity that allow researchers to estimate when key life-history events occur (Pannella, 1971). The accuracy of age and growth estimates from otoliths depends, however, on a robust relationship between otolith and somatic growth, the consistent deposition of increments at a known rate and the universal formation of checks of interest within a population (Campana, 2001). Importantly, previous studies have indicated that these assumptions do not necessarily hold for all species or age classes (Campana *et al.*, 1987; Wild *et al.*, 1995).

Daily increments have been examined in sockeye salmon *Oncorhynchus nerka* (Walbaum 1792) fry otoliths (Wilson & Larkin, 1980; Marshall & Parker, 1982) but there are no published accounts confirming the formation of daily increments in *O. nerka*

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post-smolts. Although visible marine-entry check marks have been confirmed in several *Oncorhynchus* species (Volk *et al.*, 1984; Neilson *et al.*, 1985; Zhang & Beamish, 2000; Saito *et al.*, 2007; Middleton, 2011) and marine residency in a northern population of *O. nerka* has been investigated using microchemistry techniques (Stocks *et al.*, 2014), these metrics have not been directly compared. Moreover, as freshwater residency and migration rate through estuaries vary between species and populations, the effectiveness of otolith metrics may differ as well.

Understanding this potential variation is particularly important in Pacific salmon *Oncorhynchus* species. Given that *Oncorhynchus* spp. recruitment dynamics are thought to be strongly influenced by conditions experienced shortly after ocean entry (Beamish & Mahnken, 2001), studies that can accurately estimate age and growth relative to marine-entry timing will be valuable for identifying mechanisms of mortality. In this study, the hypothesis that *O. nerka* post-smolts produce daily increments and a visible marine-entry check was tested by (1) visually validating otoliths of a known age and (2) comparing visual marine-entry check estimates with shifts in barium and strontium concentrations indicative of ocean entry.

Eggs, collected from Harrison River (49° 13' 44'' N; 121° 56' 47'' W) adult *O. nerka* in 2011, were fertilized and hatched at the University of British Columbia. Fry were then transported to the University of Victoria's Aquatic Research Facility in March 2013. Fish were smolted after transport to the University of Victoria by gradually increasing the salinity of their tanks to 29 over a period of 3 days. At both facilities, fish experienced a natural seasonal photoperiod (49° N), were fed *ad libitum* twice daily commercial fish meal pellets and reared at temperatures that varied between 10 and 16° C seasonally.

A 100 day sampling period was selected since it is a conservative estimate of the time an individual would spend migrating from southern British Columbia to southern Alaska and is thought to encompass much of the early critical period in juvenile *O. nerka* survival (Beamish & Mahnken, 2001; Beamish *et al.*, 2012). Over this period, a sub-set of the captive population was removed over 11 sampling events ( $n = 10$  individuals per event) by anaesthetizing individuals with a lethal dose of MS-222. Fish fork length ( $L_F$ ) and mass were recorded (to the nearest 1 mm and 0.1 g, respectively) and both sagittal otoliths were removed for further processing.

Otoliths (sagittae) from experimental fish were removed, rinsed in ethanol to remove remaining tissue and soaked in deionized water for 15 min. Unless the left otolith was damaged or could not be retrieved, only left sagittal otoliths were mounted and analysed. After soaking, otoliths were dried and fixed to glass microscope slides, sulcal side up, with thermoplastic adhesive (SPI Supplies Crystalbond 509; www.spi2.com). Otoliths were observed with a compound microscope (Zeiss Universal; www.zeiss/microscopy) at  $\times 25$ ,  $\times 110$  and  $\times 400$ . Images were captured with a digital camera (SPOT Flex, FX1520; www.spotimaging.com) for analysis using Image J (Rasband, 1997–2014; <http://imagej.nih.gov/ij/>). The exposed surface was polished with 30, 3 and 0.3  $\mu\text{m}$  lapping film (Digikey 3 M; www.digikey.ca) until primordia and peripheral increments could be observed along the dorsal axis. The slide was then heated, the otolith flipped and the reverse side was polished until increments and the presumed marine-entry check were clearly visible along the dorsal axis. Potential marine-entry checks were identified by the presence of an especially dark, optically dense daily increment, separated from the otolith core by a distinct translucent zone representing winter freshwater growth (the freshwater annulus). The entry check was

also separated from the otolith periphery by clearly defined increments whose spacing gradually increased, rather than the densely packed increments that preceded the first freshwater annuli (Zhang & Beamish, 2000; Saito *et al.*, 2007). If the dorsal axis of the otolith was damaged, the otolith was vateritic, or if a marine-entry check could not be identified, the otolith was discarded.

Otolith width ( $W_O$ ) was measured at the widest point along the dorsal-ventral axis. Otolith length ( $L_O$ ) was also measured, but preliminary analysis suggested that width was more strongly correlated with  $L_F$  ( $L_O$   $r^2 = 0.77$  v.  $W_O$   $r^2 = 0.81$ ). Increments between the potential check and the periphery were enumerated. The distance from primordia to observed marine-entry check (check radius) and the distance from primordia to periphery (total radius) were also recorded. All counts and measurements were performed three times per individual and the mean was used for subsequent analyses. If counts differed by more than eight daily rings, the otolith was excluded. A regression, followed by a  $\chi^2$  analysis, was used to test the null hypothesis that the slope ( $m$ ) and intercept ( $b$ ) of the relationship between predicted counts (based on known date of smolting) and observed counts were equal to one and zero, respectively (Jolicoeur, 1991; Trudel *et al.*, 2004). Statistical analyses were conducted in R 2.15 (R Core Team; [www.r-project.org](http://www.r-project.org)).

The mean  $\pm$  S.D.  $L_F$  of *O. nerka* post-smolts increased from  $93.6 \pm 17.0$  mm in the first sampling period to  $143.7 \pm 14.0$  mm in the final. Mean  $\pm$  S.D.  $W_O$  also increased from  $1277 \pm 142$  to  $1852 \pm 132$   $\mu$ m between first and final sampling periods.  $W_O$  was linearly and positively correlated with  $L_F$  ( $n = 94$ ,  $r^2 = 0.81$ ,  $P < 0.001$ ), suggesting that somatic growth can be backcalculated from otolith growth. Marine-entry checks, identified as a particularly dark increment preceded by a translucent region near the otolith periphery, were observed in all experimentally reared *O. nerka* post-smolt otoliths that were undamaged and non-vateritic along the dorsal axis ( $n = 94$ ; Fig. 1). Sixteen otoliths were discarded due to damage. Marine-entry checks did not differ substantially in appearance from those observed in Chinook salmon *Oncorhynchus tshawytscha* (Walbaum 1792) (Middleton, 2011) or chum salmon *Oncorhynchus keta* (Walbaum 1792) (Saito *et al.*, 2007). The number of increments observed was strongly correlated with the number of days since juvenile *O. nerka* were smolted, and the slope and intercept of the regression were not significantly different from zero and one, respectively ( $n = 94$ ,  $r^2 = 0.99$ ,  $m \pm \text{S.E.} = 0.99 \pm 0.01$ ,  $b \pm \text{S.E.} = 0.13 \pm 0.39$ ,  $\chi^2 = 0.21$ ,  $P > 0.05$ ). This relationship suggests that increments are formed daily in *O. nerka* for at least 100 days after smolting.

An elemental marker approach was used to validate the accuracy of visual marine entry-check estimates in post-smolts. Previous studies have indicated that strontium and barium are deposited in otoliths proportional to their environmental concentration (Bath *et al.*, 2000). As Sr is typically positively correlated and Ba is negatively correlated with salinity, the relative concentration of each of these elements in otoliths can be used to explore transitions between freshwater and marine environments (Macdonald & Crook, 2010).

Twelve otoliths from *O. nerka* post-smolts collected at sea in June and July 2007 to 2008 using a rope trawl (Tucker *et al.*, 2009) were selected to validate the formation of marine-entry checks by otolith microchemical analysis after polishing and visual measurements. Marine-entry checks were visible and appeared similar to those observed in experimentally reared juveniles. Additionally, daily increments tended to become larger and more uniformly spaced following this check. This pattern was less consistent

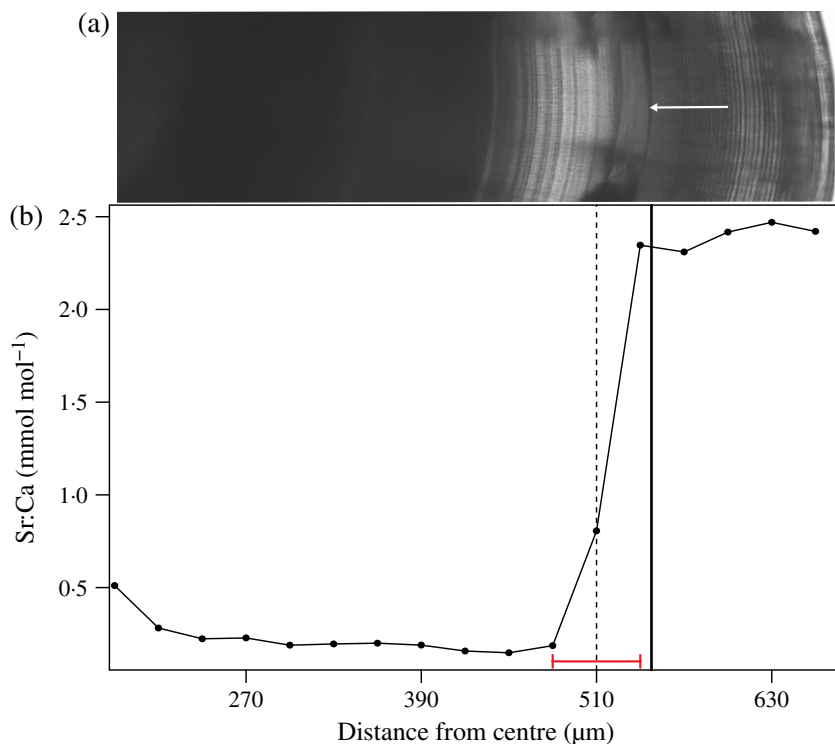


FIG. 1. Polished (a) *Oncorhynchus nerka* post-smolt otolith and (b) associated Sr:Ca profile from inductively coupled plasma mass spectrometry (ICP-MS) analysis. **▬** (a) and **|** (b), visual marine-entry check estimate. The irregular, light zone to the left of **▬** represents the freshwater annulus. ‡, chemical estimate (—)  $\pm$  95% C.I., as determined by breakpoint analysis.

in laboratory-reared post-smolts, probably due to consistent environmental conditions and food availability. DNA analyses (Beacham *et al.*, 2005) performed on these fish indicated that nine *O. nerka* post-smolts were from Great Central Lake and three from Sproat Lake (both populations enter the ocean on the west coast of Vancouver Island, British Columbia, Canada).

Elemental analysis was carried out at the University of Victoria's School of Earth and Ocean Science's inductively coupled plasma mass spectrometry (ICP-MS) Facility in Victoria, BC, with an X-Series II ICP-MS and an UP-213 laser ablation system. The laser was set at a pulse rate of 5 Hz with a 15  $\mu\text{m}$  ablation spot size and intervals of 30  $\mu\text{m}$  between ablation spot centres (except for sample 1, which had a spacing of 50  $\mu\text{m}$  between spot centres). Laser ablation occurred along the central dorsal axis of left otoliths. Prior to ablation, analyte isotopes were measured for 30 s and subtracted from those measured during ablation. Elemental concentrations were calculated using NIST 610, 613 and 615 standard glasses following methods described in the study of Miller (2007). Elemental ratios were recorded for Sr and Ba in  $\text{g kg}^{-1}$  (Ca is used as the internal standard for the analysis) and reported in  $\text{mmol mol}^{-1}$  for Sr:Ca and  $\mu\text{mol mol}^{-1}$  for Ba:Ca. One field-captured otolith was damaged during ablation and was removed from subsequent analyses.

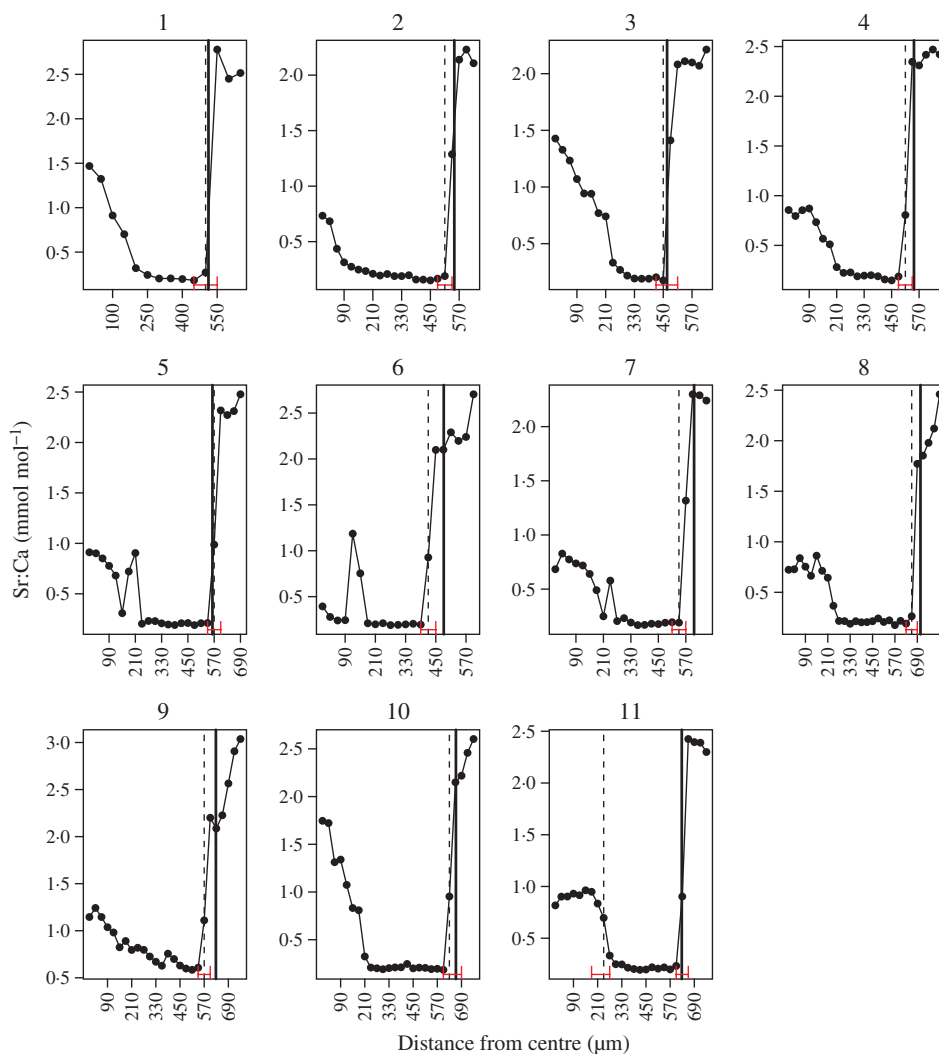


FIG. 2. Sr:Ca concentrations of ablation spots from inductively coupled plasma mass spectrometry (ICP-MS) laser transects running from *Oncorhynchus nerka* otolith primordia to dorsal periphery in 11 samples. The zone representing transition to salt water is characterized by an increase in Sr:Ca. Visual marine-entry check estimates (|), breakpoint estimates (|) and 95% C.I. (—) are indicated. Note sample 11 has two breakpoint estimates as the model failed to converge when restricted to one.

Shifts in elemental concentrations were statistically quantified by estimating breakpoints in the regression between elemental ratios and distance from otolith core. Breakpoint analysis assumes that within the classical linear regression model there are multiple segments where regression coefficients are constant and identifies locations where this relationship shifts to a new stable state (Zeileis *et al.*, 2002). Breakpoints are calculated by minimizing the residual sum of squares for each stable state of the regression model and have been previously used to quantify shifts in the elemental structure of otoliths (Stocks *et al.*, 2014). Breakpoints, along with 95% C.I.,

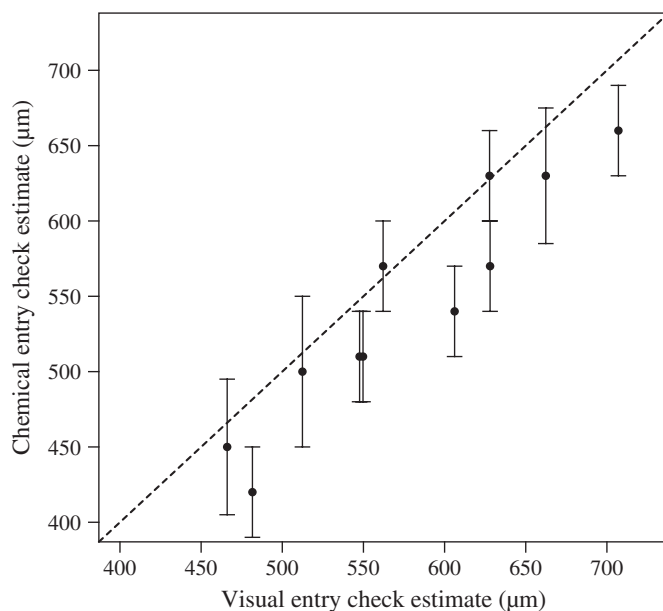


FIG. 3. Visual and chemical estimates of *Oncorhynchus nerka* marine entry measured as  $\mu\text{m}$  from the otolith core. Chemical estimates have 95% c.i. calculated using breakpoints in the regression of element concentrations across the otolith transect.

were calculated using the *strucchange* package (Zeileis *et al.*, 2002, 2003) in R. The breakpoints function in this package is built upon an algorithm for estimating multiple breakpoints described in Bai & Perron (2003) and uses a distribution function for determining c.i. from Bai (1997). When models identified multiple breakpoints in a sample (probably due to differences between otolith core, fresh water and marine zones), the breakpoint closest to the periphery was identified as the marine breakpoint and used as the marine-entry check estimate. Whether visually estimated marine-entry checks fell within the 95% c.i. of the estimated breakpoint was used to assess the accuracy of visual estimates.

In all samples of field-captured post-smolts, an increase in Sr:Ca could be observed near the otolith periphery that was consistent with saltwater entry (Figs 1 and 2); however, the breakpoint models suggested that chemical and visual marine-entry estimates varied (Fig. 3). Five visual marine-entry check estimates fell within the 95% c.i. of marine breakpoints calculated from Sr levels; the remaining visual marine-entry estimates were consistently greater than the chemical estimates, suggesting that visual entry checks were formed after Sr began to increase (Fig. 3).

Plots of Ba concentrations displayed a less consistent pattern than Sr. Although 10 otoliths displayed declines in Ba:Ca coincident with increases in Sr:Ca, breakpoint estimates could not be calculated for two samples (Fig. 4). Moreover, the majority of the otoliths examined displayed Ba declines that were strongest in the otolith core, where marine entry is highly improbable. Finally, only two samples had marine breakpoint estimates that were identical to those calculated using Sr:Ca. It is likely that these differences were caused by the extreme variation in Ba:Ca concentrations (up to three orders of magnitude) across otolith transects (Fig. 4). It is unclear why Ba:Ca estimates

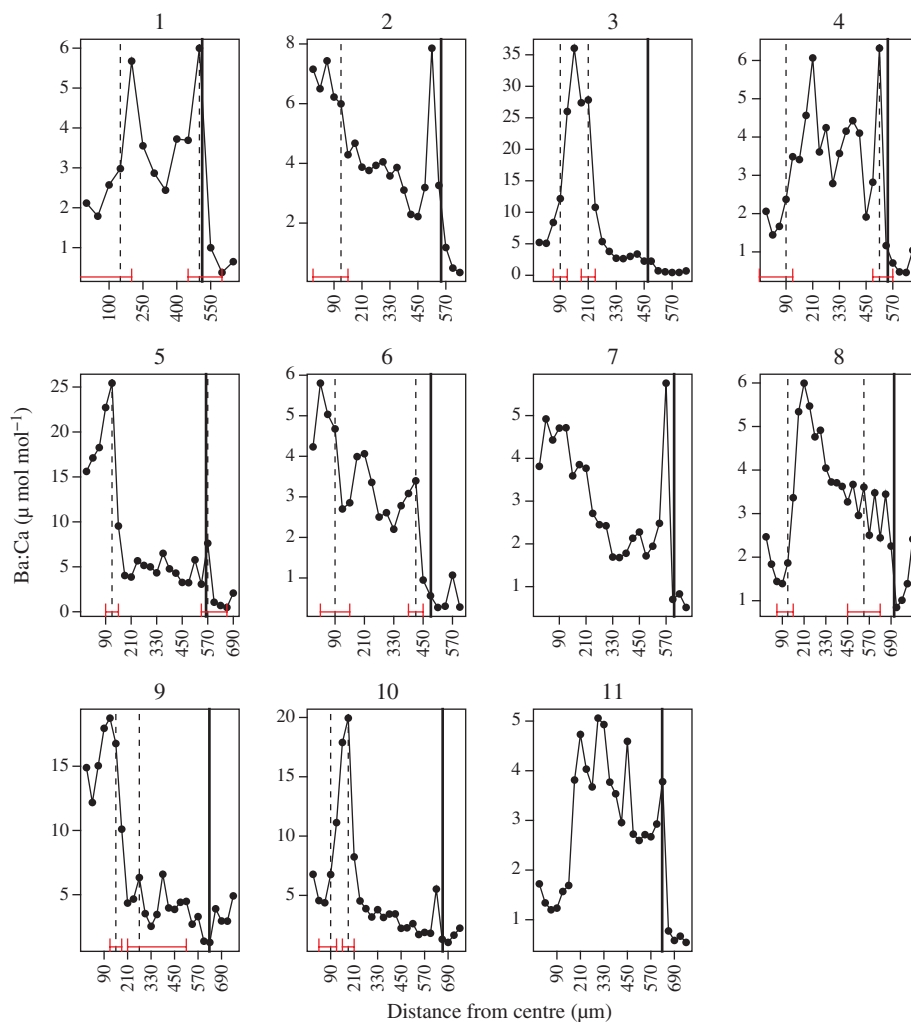


FIG. 4. Ba:Ca concentrations of ablation spots from inductively coupled plasma mass spectrometry (ICP-MS) laser transects running from otolith primordia to dorsal periphery in 11 samples. The zone representing transition to salt water is characterized by a decrease in Ba:Ca. Visual marine-entry check estimates (l), breakpoint estimates (b) and 95% c.i. (—) (absent in samples 7 and 11 as model would not converge) are indicated. Note differences in scaling of y-axis between samples representing variation in Ba:Ca within the population.

varied to such an extent; however, Ba does exhibit non-conservative mixing properties that can result in variation at scales of tens of metres and which could produce similar patterns (Li & Chan, 1979; Elsdon *et al.*, 2008). Elevated Ba levels, thought to be due to differences in elemental uptake during early life stages, have also been observed in the otolith core of several fish species (Ruttenberg *et al.*, 2005). More generally, the incorporation of Ba can shift with growth rates (Miller, 2011). Due to the large variation in Ba values and associated improbable estimates of marine-entry timing, only Sr:Ca estimates were used when making comparisons between chemical and visual estimates.



Visual marine-entry estimates that were observed after chemical estimates suggest that check formation, although correlated with environmental Sr, is not dependent on the incorporation of elemental signatures. Previous research suggests that changes to otolith composition can be temporally variable and dependent on local environmental conditions such as temperature (Miller, 2011). Although a lack of detailed water quality metrics made testing these predictions impossible, visual and marine estimates of marine residency may differ due to individual behaviour, particularly the relative rate of movement through the estuary. The field-captured post-smolts used in this study migrated through Alberni Inlet, an estuary characterized by a relatively strong vertical salinity gradient to 2–10 m depth, for at least 10 km from the river mouth (Waldichuk *et al.*, 1968). Given that juvenile *O. nerka* captured at sea are generally found at depths <10 m (Welch *et al.*, 1998), vertical or longitudinal movements through the estuary may result in Sr increases occurring prior to the formation of a visual marine-entry check. Differences in visual and chemical estimates were particularly high in otoliths with gradual increases in Sr levels (Fig. 2), suggesting that the rate at which elements are incorporated during estuarine residence varies.

Alternatively, the relatively coarse scale at which elemental data were collected may have compromised the precision of the breakpoint estimates as C.I. could only be calculated across discrete increments (*i.e.* ablation spots). As breakpoints are defined as the last observations in a segment before a shift, they will also necessarily be skewed towards earlier observations. Regardless of the mechanism driving differences in estimates, microstructural and microchemical techniques should ideally be combined for a sub-set of the sampled population to estimate potential error. Incorporating estimates of bias will be especially important when patterns of estuarine residency vary within a species.

This study indicates that for *O. nerka* post-smolts there is a strong relationship between otolith and somatic growth and that otolith increments are formed daily. Marine-entry check estimates were strongly correlated with known smolting date in experimentally reared individuals, but chemical estimates of marine entry from elemental ratios were consistently earlier than visual estimates. The results suggest that the integration of environmental chemical signatures and the formation of microstructures in otoliths, although correlated, fundamentally reflect different physiological processes that may ultimately be influenced by individual behaviour. Future studies may benefit from integrating chemical and structural techniques, especially if precise estimates of marine entry are necessary.

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