

A simple method to assess the marine environment residence duration of juvenile sockeye salmon (*Oncorhynchus nerka*) using laser ablation

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Abstract: Monitoring habitat utilization and early marine growth of sockeye salmon juveniles (*Oncorhynchus nerka*) in fjords of the Pacific Northwest is currently hampered by difficulties in estimating residence times, limiting scientific advances in certain aspects of this species' fisheries management and conservation. Combining otolith microchemistry and conventional daily ring counts, we were able to obtain the date of first entry and the residence time of sockeye juveniles in Rivers Inlet, British Columbia. This operationally inexpensive method builds upon variable microelement concentrations in fresh- and saltwater environments: barium (Ba) and strontium (Sr) concentrations within the sockeye otoliths differed between the freshwater and seawater growth zones; Ba concentrations in the freshwater growth zone were significantly higher than those in the seawater growth zone, while Sr concentrations in the former were significantly lower than in the latter. The concentrations of these elements within otoliths were determined quantitatively at high spatial resolution using *in situ* laser ablation inductively coupled with a plasma mass spectrometer (ICPMS) providing a record of the ambient environmental conditions experienced by individual fish. Exploratory analysis of a 3-year data set showed that the mean residence time of sockeye juveniles in Rivers Inlet varied between 3 and 6 weeks between years.

Résumé : Des difficultés associées à l'estimation des temps de séjour font entrave à la surveillance de l'utilisation de l'habitat et du début de la croissance en mer des saumons sockeyes (*Oncorhynchus nerka*) juvéniles dans les fjords du nord-ouest du Pacifique, ce qui limite les avancées scientifiques concernant certains aspects de la gestion et de la conservation de cette espèce. En combinant la microchimie des otolites à la méthode conventionnelle de décompte des anneaux quotidiens, nous avons obtenu la date de première entrée et le temps de séjour de saumons sockeyes juvéniles dans le bras de mer Rivers, en Colombie-Britannique. Cette méthode d'application peu coûteuse est basée sur la variabilité des concentrations de microéléments dans les milieux d'eau douce et salée. Les concentrations de baryum (Ba) et de strontium (Sr) dans les otolites de saumons sockeyes de zones de croissance en eau douce et en eau salée étaient différentes; les concentrations de Ba dans la zone de croissance en eau douce étaient significativement plus grandes que celles de la zone de croissance en eau salée, alors que pour les concentrations de Sr, c'était plutôt l'inverse. Les concentrations de ces éléments dans les otolithes ont été déterminées de manière quantitative à une haute résolution spatiale par ablation au laser jumelée à un spectromètre de masse à source à plasma inductif (ICPMS), fournissant ainsi un registre des conditions ambiantes rencontrées par chaque poisson. L'analyse préliminaire d'un ensemble de données recueillies sur une période de 3 ans a montré que le temps de séjour moyen des saumons sockeyes juvéniles dans le bras de mer Rivers était de 3 à 6 semaines selon l'année. [Traduit par la Rédaction]

Introduction

The sockeye salmon (*Oncorhynchus nerka*) is a large teleost fish widely distributed in coastal water throughout the North Pacific Ocean. It is an anadromous species utilizing both freshwater and marine habitats, for spawning-larval development and growth-maturation, respectively (Quinn et al. 2009). Growth during the early marine phase is critical to recruitment because of size-selective juvenile mortality (Koenings et al. 1993; McKinnell et al. 2001; Farley et al. 2007; Welch et al. 2011). Quantifying the importance of the early marine period to sockeye salmon growth and development is contingent upon accurate estimates of the length of time that individual fish spend in different habitats. Otoliths, structures that are composed of calcium carbonate and contained in the endolymphatic sac of teleost fish, grow throughout a fish's life (Gauldie and Nelson 1990). On average, sockeye salmon accrete otolith rings on a daily basis (Wilson and Larkin 1980). The

elemental composition of the otolith reflects that of the water in which the fish lives, and as otolith rings accrete, a change can be seen in certain trace elements within the otolith when the fish encounters new conditions (Phillis et al. 2011). Evidence exists for strong inverse correlations of Sr:Ca and Ba:Ca ratios in response to changing environmental conditions (Elsdon and Gillanders 2002; McCulloch et al. 2005). During the freshwater phase, fish otoliths' Sr:Ca ratios are low and Ba:Ca ratios are high, while the opposite is true during the marine phase (McCulloch et al. 2005). It is therefore expected that the Sr:Ba ratio should change significantly during the juvenile salmon transition from fresh water to salt water (Campana et al. 1994). The application of laser ablation inductively coupled with a plasma mass spectrometer (ICPMS) offers to provide remarkable resolution of elemental concentrations across an otoliths surface, thus providing a complete record of exposure to previous environments (Campana 1999).

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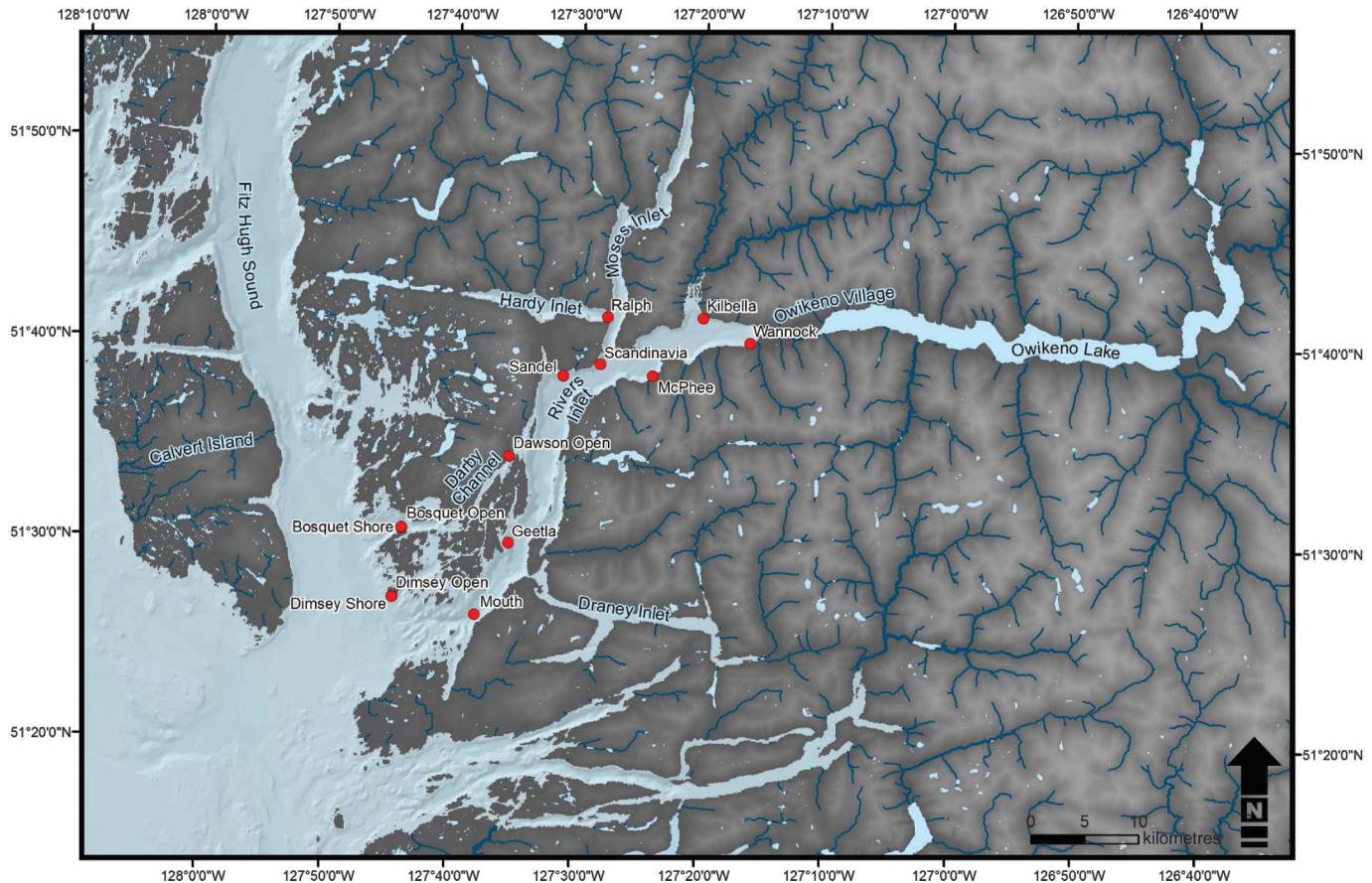
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Fig. 1. Map of Rivers Inlet. Possible outmigration routes for the sockeye smolts are (i) down the more protected Darby Channel into the Fitz Hugh Sound or (ii) through the main Rivers Inlet channel into the Queen Charlotte Sound. Dots indicate the location of the 13 seining stations sampled fortnightly from late April to early July in 2008, 2009, and 2010.



The aim of this study was to develop an operationally inexpensive and effective method of assessing the date of first entry and the residence time of sockeye juveniles in the early marine phase using otolith microchemistry, derived from laser ablation ICPMS, and conventional aging approaches. We used Rivers Inlet, British Columbia, as a test system (Fig. 1). Rivers Inlet sockeye spend two winters in Owikeno Lake before migrating to the Pacific Ocean via the Wannock River and the Rivers Inlet fjord. Rivers Inlet is approximately 40 km long and 3 km wide and averages 200–300 m deep and beyond a relatively deep sill at its mouth opens into Queen Charlotte Sound (Fig. 1). The fjord is characterized by an estuarine circulation due to the Wannock River outflow, which is strongest during the freshet in early Summer (May–July), coinciding with the outmigration of sockeye smolt. During this time a pronounced shallow halocline (~5 m) is established with salinity of 25–30, which can extend more than half the length of the inlet (Hodal 2011). Currently, the residence time of juvenile sockeye salmon in Rivers Inlet is unknown but assumed to be 1–3 weeks (Buchanan 2006; Ajmani 2011). It is therefore not possible to estimate inlet growth rates, how these may vary from year to year, and their relationship to physical factors and prey availability.

Methodology

Otolith collection, extraction, and storage

Juvenile sockeye salmon were collected in Rivers Inlet from May to July 2008, 2009, and 2010 (Table 1), using a 364 m long by 29 m deep seine net, with a mesh size of 2.5 to 3.75 cm and a 0.6 cm knotless bunt. The net was provided by the Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, British Columbia,

and deployed from the MV *Western Bounty*. Specimens were immediately preserved at -20 °C. In the laboratory they were measured (fork length) and weighed (wet mass), and otoliths were extracted (both left and right) to Eppendorf tubes. The 2008 otoliths were stored in ethanol, while 2009 and 2010 otoliths were sealed in air alone. All samples were kept at 4 °C. Six right-side otoliths from each year were used for this study and were chosen from the largest fish caught, generally collected from the mouth of the inlet (Table 1).

A total of 10 sites were surveyed, spaced along the length of Rivers Inlet. Sockeye smolts in Rivers Inlet have two possible outmigration routes: a southern route out of the main Rivers Inlet channel into the Queen Charlotte Sound or down the Darby Channel (Fig. 1). The mean size of smolt increases from the head to the mouth of the inlet, indicating a linear passage down the length of the inlet during which time their mass increases at least fourfold (Ajmani 2011). For this preliminary study, we primarily used samples collected near the mouth of the inlet (Dimpsey Shore, Dimpsey Open, Bosquet Open, and Bosquet Shore) to provide estimates of total inlet residence time (Fig. 1).

Mounting and polishing otoliths

Otoliths were rinsed with Milli-Q water to remove any excess membrane and mounted on slides using crystal-bond thermoplastic adhesive. The otolith orientation was corrected to ensure that the rounded side of the otolith was facing down before the crystal-bond hardened. Otoliths were polished using 30 µm Imperial Lapping Film lubricated with Milli-Q water. Using a Nikon Eclipse tE 2000-S inverted ocular microscope, the otolith was repeatedly examined

Table 1. Information on fish collected during 2008–2010 in Rivers Inlet and laser ablation results of sockeye smolts.

Fish ID	Collection date	Station*	SL (mm)	TL (mm)	WM (g)	Otolith length (mm)	Otolith width (mm)	Seawater zone (μm)	Ring width (μm)	1 SD	Time spent in the inlet (days)			Distance from head (km)	Travel speed ($\text{km} \cdot \text{day}^{-1}$)			
											Min.	Mean	Max.		Min.	Mean	Max.	
08_04	27 May 2008	Dimpsey Shore	91.0	106.0	8.32	1.7766	1.2088	27.15	2.30	0.44	9.9	11.8	14.5	15 May 2008	42	2.9	3.6	4.2
08_05	9 June 2008	Dimpsey Shore	92.0	102.5	8.65	1.9341	1.3278	39.99	1.87	0.28	18.6	21.4	25.1	19 May 2008	42	1.7	2.0	2.3
08_07	9 June 2008	Dimpsey Shore	97.0	110.0	10.11	1.6996	1.2857	96.16	3.13	0.74	24.9	30.7	40.2	10 May 2008	42	1.0	1.4	1.7
08_08	9 June 2008	Dimpsey Open	99.5	117.5	12.78	1.9780	1.3626	47.05	2.23	0.50	17.2	21.1	27.2	20 May 2008	42	1.5	2.0	2.4
08_09	27 May 2008	Bosquet Shore	104.0	121.0	14.31	2.0440	1.3810	28.30	1.75	0.30	13.8	16.2	19.6	12 May 2008	38	1.9	2.3	2.8
08_10	9 June 2008	Dimpsey Shore	87.0	99.0	7.81	1.7246	1.1537	37.01	2.04	0.38	15.3	18.2	22.4	22 May 2008	42	1.9	2.3	2.7
09_01	28 June 2009	Bosquet Open	92.0	104.0	8.16	1.9040	1.2735	62.69	1.61	0.22	34.2	38.9	45.1	21 May 2009	38	0.8	1.0	1.1
09_02	28 June 2009	Bosquet Open	113.0	126.0	17.41	2.2601	1.5165	92.76	2.35	0.58	31.7	39.5	52.3	20 May 2009	38	0.7	1.0	1.2
09_03	12 June 2009	Bosquet Shore	87.0	100.5	6.71	1.7473	1.2674	52.87	2.28	0.54	18.8	23.2	30.3	21 May 2009	38	1.3	1.6	2.0
09_07	28 June 2009	Dawsons Open	91.0	107.0	8.76	1.6813	1.2198	59.51	1.60	0.14	34.3	37.3	40.9	23 May 2009	25	0.6	0.7	0.7
09_08	28 June 2009	Dawsons Open	97.0	112.0	9.80	1.7399	1.2747	51.52	2.00	0.24	23.0	25.8	29.4	3 June 2009	25	0.9	1.0	1.1
09_09	29 June 2009	Scandinavia	92.5	106.0	8.36	1.9121	1.3480	56.67	3.11	0.83	14.4	18.2	24.8	12 June 2009	14	0.6	0.8	1.0
09_10	28 June 2009	Mouth	84.0	92.0	7.80	1.7253	1.2821	46.51	2.40	0.59	15.6	19.4	25.6	9 June 2009	35	1.4	1.8	2.2
10_01	5 July 2010	Dimpsey Open	104.0	119.5	14.85	1.8315	1.4432	97.15	1.84	0.41	43.2	52.8	68.0	14 May 2010	42	0.6	0.8	1.0
10_02	5 July 2010	Dimpsey Shore	104.0	113.0	15.37	2.0220	1.3626	100.16	1.82	0.30	47.3	55.0	65.8	12 May 2010	42	0.6	0.8	0.9
10_03	3 June 2010	Bosquet Open	105.0	116.0	14.71	1.9963	1.4103	51.40	2.29	0.36	19.4	22.4	26.7	12 May 2010	38	1.4	1.7	2.0
10_04	5 July 2010	Dimpsey Shore	110.0	120.0	17.01	1.9377	1.4212	104.41	2.17	0.25	43.1	48.1	54.5	19 May 2010	42	0.8	0.9	1.0
10_09	27 June 2010	Dimpsey Shore	100.5	115.0	13.22	1.8608	1.3077	112.01	2.31	0.37	41.8	48.5	57.7	10 May 2010	42	0.7	0.9	1.0
10_10	5 July 2010	Bosquet Open	99.0	116.0	13.24	1.8938	1.3407	70.88	2.91	0.45	21.1	24.4	28.8	11 June 2010	38	1.3	1.6	1.8

Note: SL, standard length; TL, total length; WM, wet mass.

*Sampling station position: Dimpsey Shore: 51.559°N, 127.606°W; Dimpsey Open: 51.447°N, 127.745°W; Bosquet Shore: 51.512°N, 127.734°W; Bosquet Open: 51.515°N, 127.734°W; Dawsons Open: 51.574°N, 127.586°W; Scandinavia: 51.645°N, 127.467°W; Mouth: 51.441°N, 127.632°W.

for possible over-polishing. Once the rings were adequately revealed, the sample was polished to remove surface scratches using 3 μm Imperial Lapping Film. Each otolith was photographed and a scale was applied to record its length (longest distance from anti-rostral to rostral ends) and width (longest distance perpendicular to length). The photographs were later used to establish the optimal area for laser ablation.

Laser ablation measurements

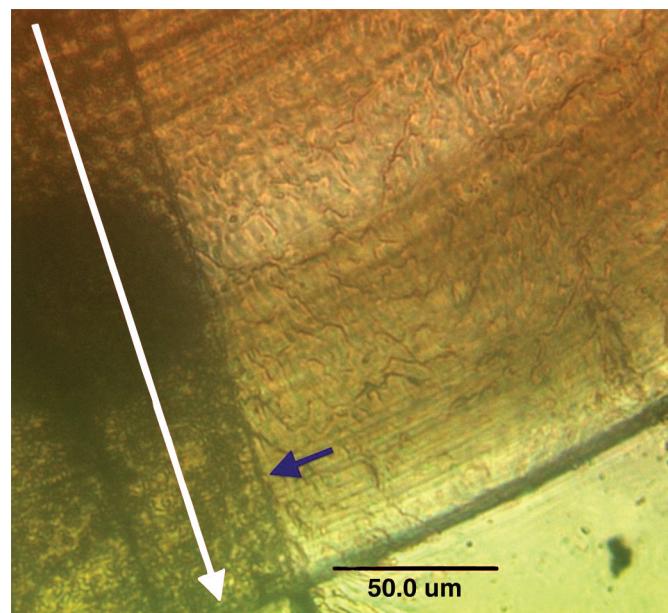
Each samples was run through a Fisher Scientific FS30 ultrasonic bath containing Milli-Q water for 3 min to remove surface contamination. The samples were then analyzed using a Resonetics M50-LR Ablation System Coherent ARF laser, frequency-quadrupled to 190 nm, connected to an Agilent Technologies 7700 Series Quadrupole ICPMS system. The system ran a computer-controlled XY translation stage at 0.25 μm resolution, and the samples were viewed live through a video microscope on the computer screen. Two slides were placed in the sample cell and the laser was recalibrated for drift correction and accuracy before and after sampling the otoliths using NIST 6-12 glass and a Ca internal standard. The laser was programmed to raster a 2 $\mu\text{m} \times 150 \mu\text{m}$ line using a high-resolution slit with a repetition rate of 20 Hz and laser energy of 120 mJ with 4 $\text{J}\cdot\text{cm}^{-3}$ fluence. Ablation was undertaken in a He atmosphere with a 750 $\text{mL}\cdot\text{min}^{-1}$ flow rate. N_2 gas was added at 2.8 $\text{mL}\cdot\text{min}^{-1}$ to improve ICPMS sensitivity. Ejecta were transported to the torch of the ICPMS in an Ar gas flow with a carrier flow rate of 64 $\text{L}\cdot\text{min}^{-1}$. Data were collected for several trace elements, namely ^{43}Ca , ^{44}Ca , ^{88}Sr , ^{138}Ba , ^{24}Mg , ^9Be , ^{11}B , ^{29}Si , ^{55}Mn , ^{57}Fe , and ^{238}U . A dwell time of 340 μs was applied for ^{43}Ca , ^{88}Sr , and ^{138}Ba , and a 20 μs dwell time was applied for the rest of the elements. Sr:Ca and Ba:Ca ratios are recommended for studying migrations between marine and freshwater environments (McCulloch et al. 2005) and thus were used in this study. Remaining measured elements have been considered as poor indicators of environmental changes and consequently were not used in this study (Elsdon and Gillanders 2002).

Data reduction and analysis

ICPMS is a time-resolved analytical technique that is subject to matrix effects, sensitivity drift, and other effects (Longerich et al. 1996). As previously mentioned, a Ca internal standard was used to mitigate a large number of these effects. The count rates of trace elements in the otolith (Sr, Mg, Ba, etc.) were rationed to the concentration of Ca (the internal standard). By measuring the same ratio (e.g., Sr:Ca) in standard material (NIST 6-12 glass), it was then possible to calculate the concentration of the unknown element in the sample. In many cases in the literature, Sr and Ba are reported as Sr:Ca and Ba:Ca ratios, since they are calculated in parts per million of Ca. Henceforward, they will be referred to as Sr and Ba concentrations, but are comparable to Sr:Ca and Ba:Ca ratios in the literature.

The transition from fresh water to marine, or the marine entry point, is a major change in the juvenile sockeyes' environmental history, which is expected to be reflected by a sharp change (breakpoint) in otolith chemistry. Segmented regression analysis (SRA) is a method of regression analysis in which the independent variable is partitioned into intervals and a separate line segment is fit to each interval. We used SRA to quantify the change in Sr:Ba in response to distance across the otoliths. The least-squares method was applied separately to the freshwater and marine segments, and two regression lines were made to fit the data set as closely as possible. Several statistical tests were used to determine the type of trend, as well as the significance of the breakpoint (standard error of the breakpoint, *t* tests, correlation coefficient, and ANOVA analysis). "SegReg", a program developed to run SRAs, was used to determine the marine entry point using Sr:Ba graphs (Oosterbaan 2011). The program determines breakpoint within 90% confidence interval and up to 99.99% significance according to ANOVA (Oosterban 2011).

Fig. 2. Example of otolith daily rings of the fish 8_10 noticeable as dark lines perpendicular to the laser ablation path, which can be seen in the left of the photo (path indicated by arrow descending from upper left corner). The smaller arrow indicates the marine entry point, 37.01 μm from the edge of the otolith.



Otolith rings were measured within the estuarine growth zone, as proximal to the laser path as possible. This was accomplished by using a Nikon Eclipse TE 2000-S inverted ocular microscope connected via a camera to AutoMontagePro, a computer program. At 400 \times magnification, otolith rings were identified and the width of the rings was measured using a digital measurement tool (Fig. 2). In some cases, the rings were very hard to identify, resulting in a smaller sample size. The length of time spent in Rivers Inlet by the sockeye smolt was then determined by dividing the length of otolith identified as the seawater zone by the mean otolith ring width, which is the equivalent of 1 day. Sockeye smolt travel speeds were determined by dividing the length of the inlet travelled by the time spent in the inlet.

Results and discussion

A total of 19 otoliths were assayed and concentrations of Sr and Ba were recorded. Profiles of the changes in these concentrations from the inner otolith toward the outer edge (following path shown in Fig. 2) revealed a significant change in Sr and Ba concentrations, and example plots are presented for each year in Figs. 3 to 5.

During the early freshwater phase, preserved closer to the otolith center, low Sr concentrations (10–20 ppm) and high Ba concentrations (0.2–0.5 ppm) were observed (panels *a* and *b* in Figs. 3–5). Conversely, during the marine phase, recorded in the outermost zone of the otolith, the opposite situation was observed with high Sr concentrations of 50–100 ppm and low Ba concentrations of <0.1 ppm (panels *a* and *b* in Figs. 3–5). The change in Sr and Ba concentrations was well captured by Sr:Ba ratios. During the freshwater phase, the Sr:Ba ratio was generally low (30–60), while in the seawater phase the ratio was >1000 (Figs. 3c, 4c, 5c; Appendix A). The variability in Sr:Ba during the marine phase appeared to be attributed to Sr concentrations, probably reflecting variability in salinity in the upper water column. However, despite this variability, the freshwater and marine phases were clearly separated in chemical composition.

The results of the SRA revealed quite a range of otolith marine zone widths. The shortest seawater zone was 27.15 μm (sample 08_4), while the longest was 112.01 μm (sample 10_9; Table 1). Because days

Fig. 3. (a) Strontium concentration, (b) barium concentration, and (c) Sr:Ba profiles for otolith sample 08_08.

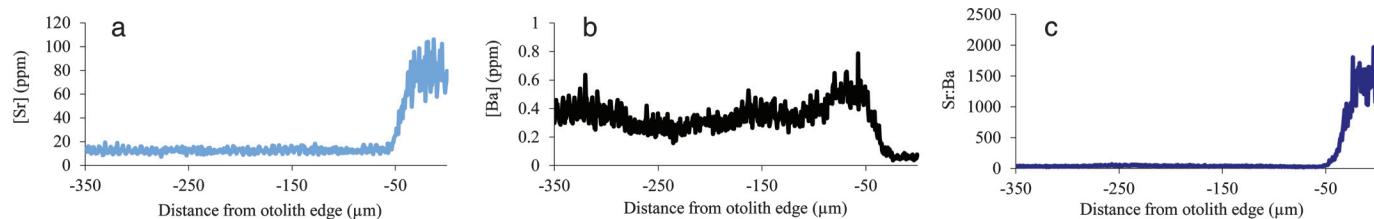


Fig. 4. (a) Strontium concentration, (b) barium concentration, and (c) Sr:Ba profiles for otolith sample 09_01.

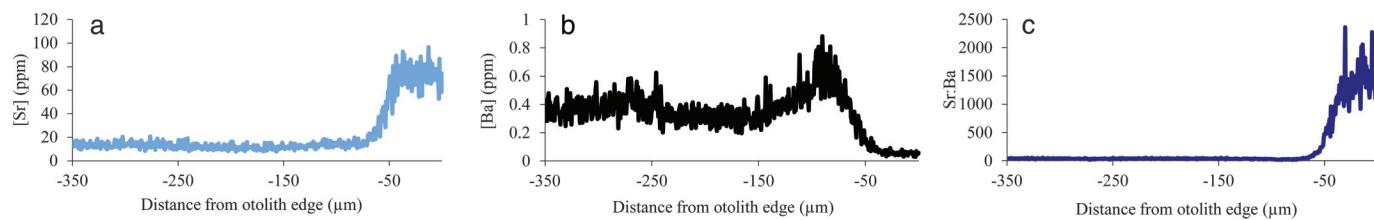
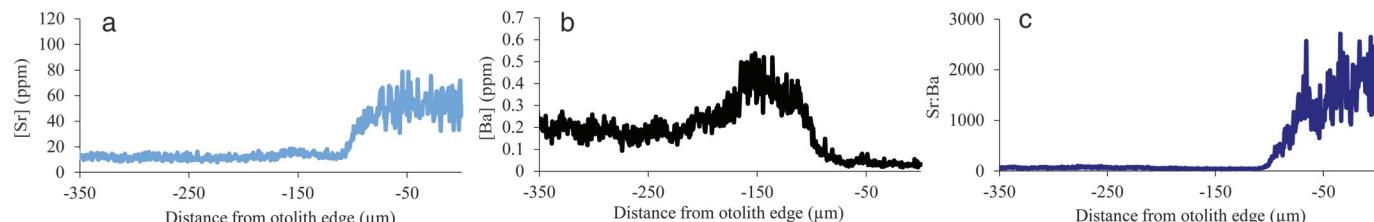


Fig. 5. (a) Strontium concentration, (b) barium concentration, and (c) Sr:Ba profiles for otolith sample 10_04.



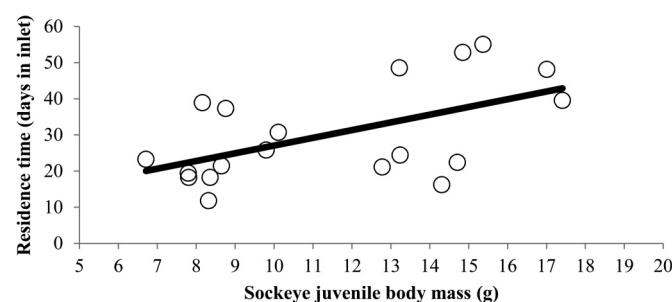
in the inlet could be subject to error in ring width estimates, we calculated minimum duration based on the ring width plus one standard deviation and maximum duration using the ring width minus one standard deviation (Table 1). According to our preliminary findings, the date of first entry of Rivers Inlet sockeye smolt was highly consistent, 10 May through to 12 June, between years. The smolt spent on average 12 to 31 days (mean 20 days), 18 to 40 days (29 days), and 22–55 days (42 days) in the inlet during 2008, 2009, and 2010, respectively (Table 1), and traveled through the inlet at a mean speed ranging from 0.7 to 4.2 km·day⁻¹ (Table 1). Across all 3 years, there was a general positive correlation between the smolt mass and the residence time in the inlet (Fig. 6). It should be noted that since we are unsure of whether the smolt delayed their outward migration at the inlet mouth, our estimates of inlet residence time may be overestimates. However, the values indicated total length of the smolt estuarine–marine phase.

Sr:Ba fingerprints are diagnostic of their particular terrestrial environment and are clearly distinct between freshwater and marine systems (McCulloch et al 2005). While previous studies have estimated that sockeye smolt spend approximately 1–3 weeks in Rivers Inlet, using otoliths Sr:Ba ratios gave residence time estimates of 3–7 weeks, with substantial variation between years. Since our study focused only on larger smolt sizes, our residence time estimates may be on the high end of the spectrum. Crucially, the methodology presented here provided an effective means of assessing the residence time of sockeye juveniles in the early marine phase of their life cycle. As such, it represents a valuable tool to investigate juvenile sockeye salmon growth rates and their drivers, which in turn may provide fresh insights into interannual fluctuations in stock recruitment.

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Fig. 6. Relationship between fish mass and time spent in Rivers Inlet. This plot indicates that a positive relationship exists between the two variables.



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Appendix A

Appendix figures showing Sr:Ba curves for 19 different locations and dates appear on the following pages.

Fig. A1. Sample 8_04, caught at Dimpsey Shore on 27 May 2008. Seawater growth zone 27.15 μm , time spent in inlet 9.9–14.5 days, travel speed 2.9–4.2 $\text{km}\cdot\text{day}^{-1}$.

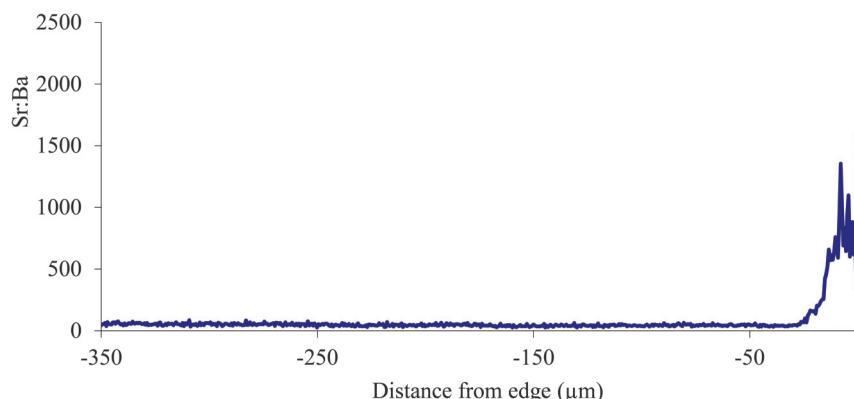


Fig. A2. Sample 8_05, caught at Dimpsey Shore on 9 June 2008. Seawater growth zone 39.99 μm , time spent in inlet 18.6–25.1 days, travel speed 1.7–2.3 $\text{km}\cdot\text{day}^{-1}$.

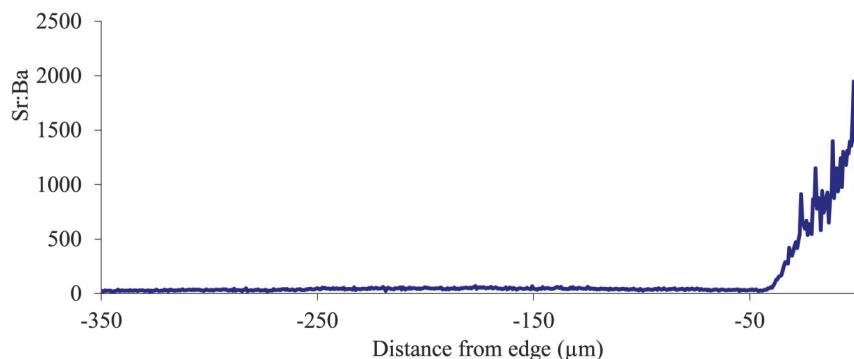


Fig. A3. Sample 8_07, caught at Dimpsey Shore on 9 June 2008. Seawater growth zone 96.16 μm , time spent in inlet 24.9–40.2 days, travel speed 1.0–1.7 $\text{km}\cdot\text{day}^{-1}$.

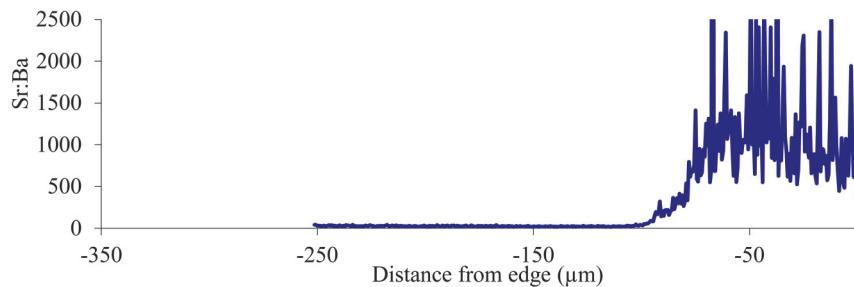


Fig. A4. Sample 8_08, caught at Dimpsey Open on 9 June 2008. Seawater growth zone 47.05 μm , time spent in inlet 17.2–27.2 days, travel speed 1.5–2.4 $\text{km}\cdot\text{day}^{-1}$.

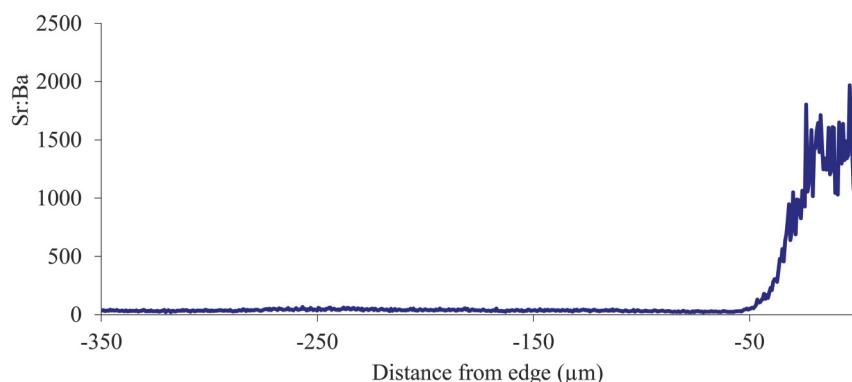


Fig. A5. Sample 8_09, caught at Bosquet Shore on 27 May 2008. Seawater growth zone 28.3 μm , time spent in inlet 13.8–19.6 days, travel speed 1.9–2.8 $\text{km}\cdot\text{day}^{-1}$.

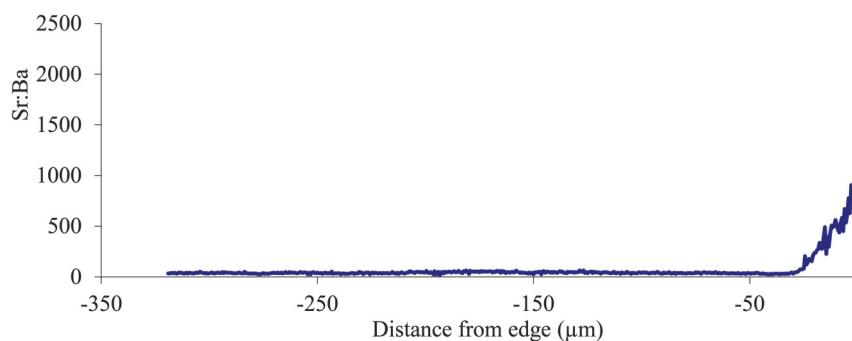


Fig. A6. Sample 8_10, caught at Dimpsey Shore on 9 June 2008. Seawater growth zone 37.01 μm , time spent in inlet 15.3–22.4 days, travel speed 1.9–2.7 $\text{km}\cdot\text{day}^{-1}$.

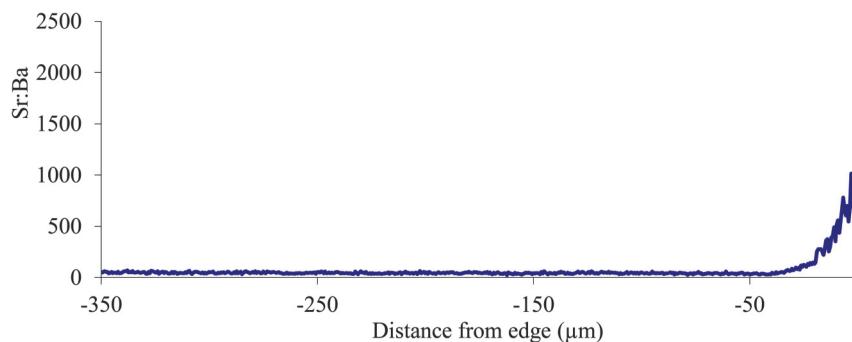


Fig. A7. Sample 9_01, caught at Bosquet Open on 28 June 2009. Seawater growth zone 62.69 μm , time spent in inlet 34.2–45.1 days, travel speed 0.8–1.1 $\text{km}\cdot\text{day}^{-1}$.

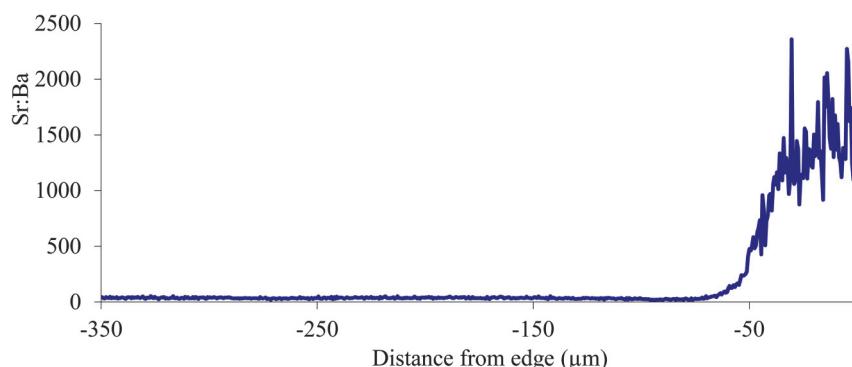


Fig. A8. Sample 9_02, caught at Bosquet Open on 28 June 2009. Seawater growth zone 92.76 μm , time spent in inlet 31.7–52.3 days, travel speed 0.7–1.2 $\text{km}\cdot\text{day}^{-1}$.

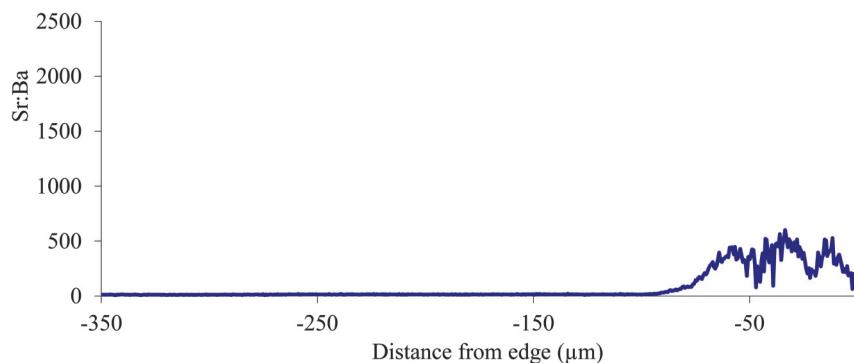


Fig. A9. Sample 9_03, caught at Bosquet Shore on 12 June 2009. Seawater growth zone 52.87 μm , time spent in inlet 18.8–30.3 days, travel speed 1.3–2.0 $\text{km}\cdot\text{day}^{-1}$.

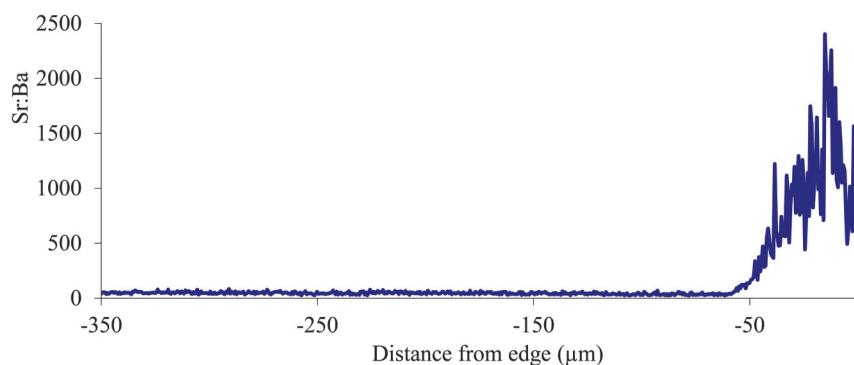


Fig. A10. Sample 9_07, caught at Dawsons Open on 28 June 2009. Seawater growth zone 59.51 μm , time spent in inlet 34.3–40.9 days, travel speed 0.6–0.7 $\text{km}\cdot\text{day}^{-1}$.

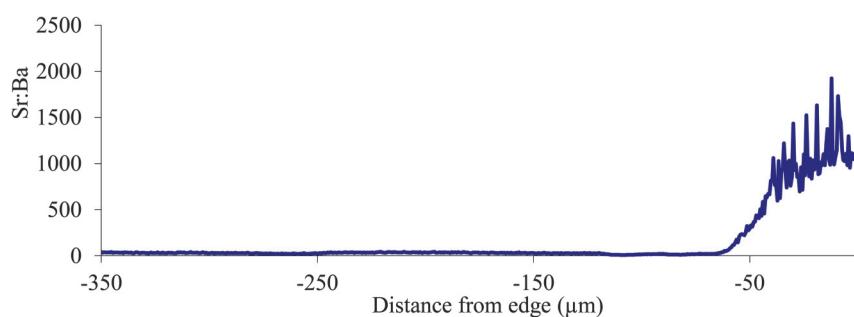


Fig. A11. Sample 9_08, caught at Dawsons Open on 28 June 2009. Seawater growth zone 51.52 μm , time spent in inlet 23–29.4 days, travel speed 0.9–1.1 $\text{km}\cdot\text{day}^{-1}$.

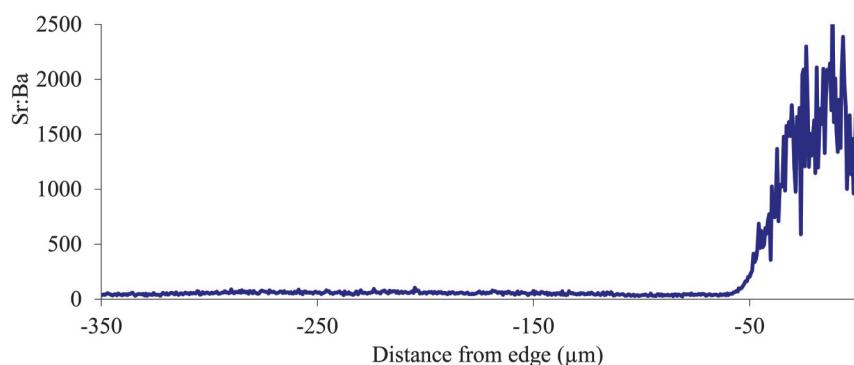


Fig. A12. Sample 9_09, caught at Scandinavia on 29 June 2009. Seawater growth zone 56.67 μm , time spent in inlet 14.4–24.8 days, travel speed 0.6–1.0 $\text{km}\cdot\text{day}^{-1}$.

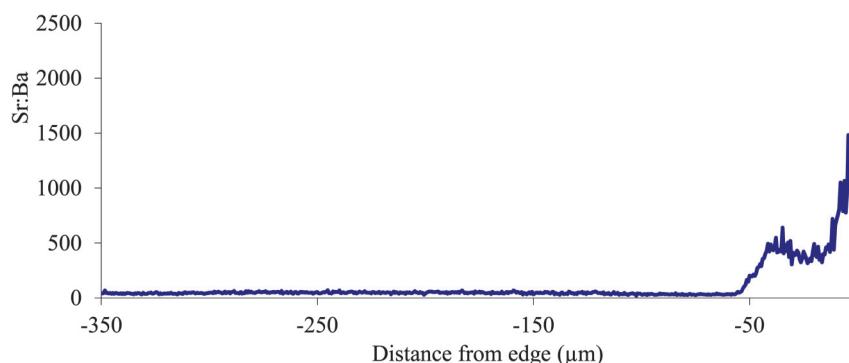


Fig. A13. Sample 9_10, caught at Mouth on 28 June 2009. Seawater growth zone 46.51 μm , time spent in inlet 15.6–25.6 days, travel speed 1.4–2.2 $\text{km}\cdot\text{day}^{-1}$.

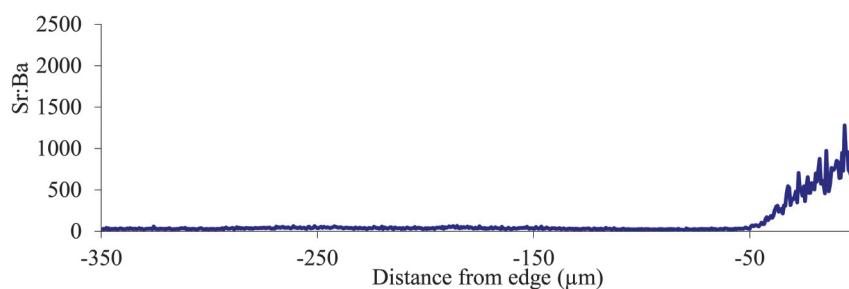


Fig. A14. Sample 10_01, caught at Dimpsey Open on 5 July 2010. Seawater growth zone 97.15 μm , time spent in inlet 43.2–68 days, travel speed 0.6–1.0 $\text{km}\cdot\text{day}^{-1}$.

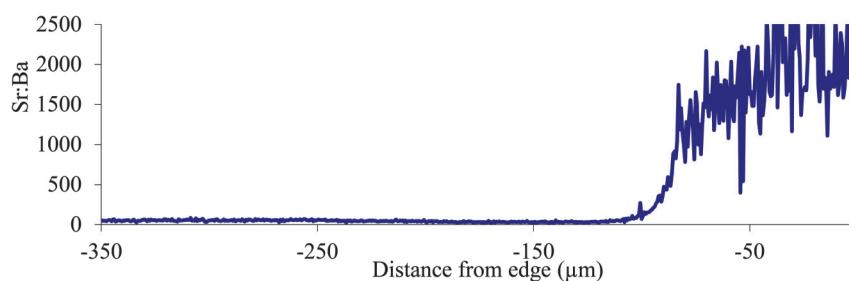


Fig. A15. Sample 10_02, caught at Dimpsey Shore on 5 July 2010. Seawater growth zone 100.16 μm , time spent in inlet 47.3–65.8 days, travel speed 0.6–0.9 $\text{km}\cdot\text{day}^{-1}$.

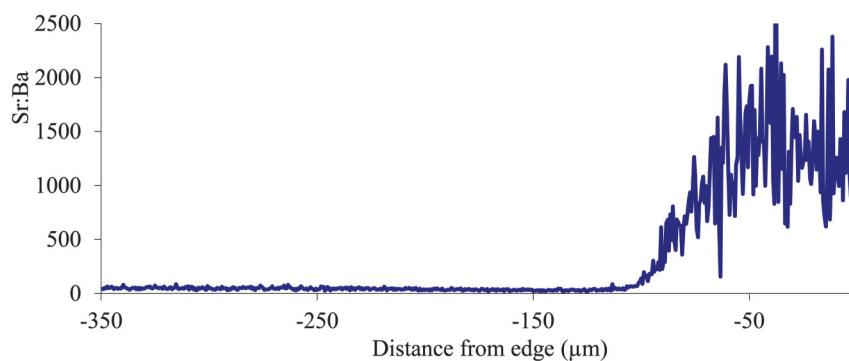


Fig. A16. Sample 10_03, caught at Bosquet Open on 3 July 2010. Seawater growth zone 51.4 μm , time spent in inlet 19.4–26.7 days, travel speed 1.4–2.0 $\text{km}\cdot\text{day}^{-1}$.

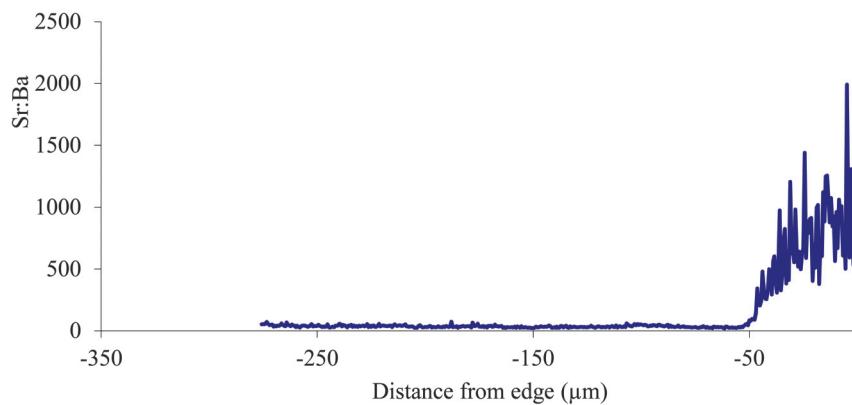


Fig. A17. Sample 10_04, caught at Dimpsey Shore on 5 July 2010. Seawater growth zone 104.41 μm , time spent in inlet 43.1–54.5 days, travel speed 0.8–1.0 $\text{km}\cdot\text{day}^{-1}$.

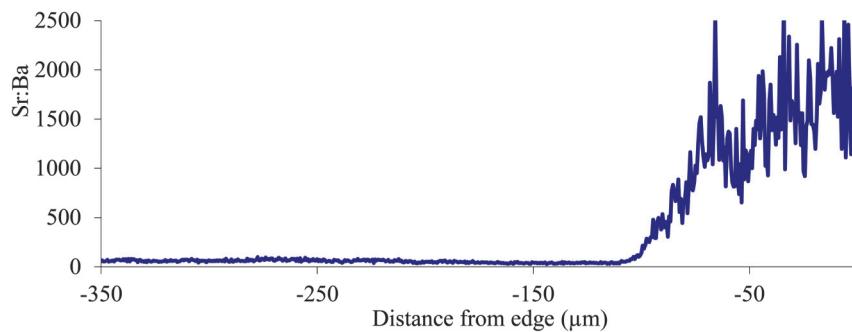


Fig. A18. Sample 10_09, caught at Dimpsey Shore on 27 June 2010. Seawater growth zone 112.01 μm , time spent in inlet 41.8–57.7 days, travel speed 0.7–1.0 $\text{km}\cdot\text{day}^{-1}$.

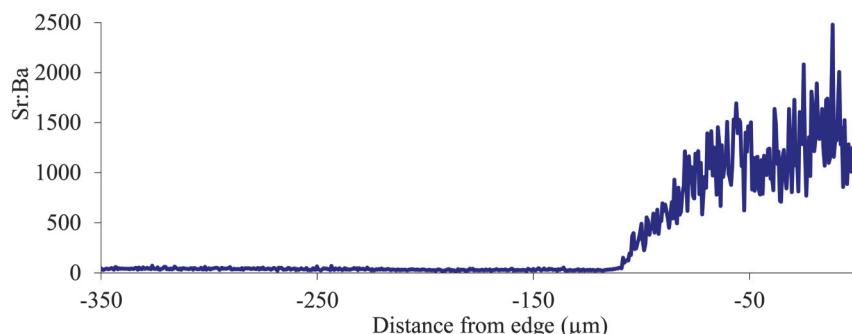


Fig. A19. Sample 10_10, caught at Bosquet Open on 5 July 2010. Seawater growth zone 70.88 μm , time spent in inlet 21.1–28.8 days, travel speed 1.3–1.8 $\text{km}\cdot\text{day}^{-1}$.

