

## Life history and age at maturity of an anadromous smelt, the eulachon *Thaleichthys pacificus* (Richardson)

A. D. CLARKE\*†, A. LEWIS‡, K. H. TELMER§  
AND J. M. SHRIMPTON\*

\*Ecosystem Science & Management Program, University of Northern British Columbia, Prince George, British Columbia, V2N 4Z9, Canada, †Ecofish Research Ltd, Courtenay, British Columbia, V9N 1N5, Canada and §School of Earth and Ocean Sciences, University of Victoria, Victoria, British Columbia, V8W 3P6, Canada

(Received 24 January 2007, Accepted 15 June 2007)

Trace element and fork length ( $L_F$ ) frequency analyses of eulachon *Thaleichthys pacificus* otoliths were used to determine age at maturity and repeat spawning potential, two aspects of eulachon life history that are not known but are important for successful management of this species. The  $L_F$ -frequency analysis for ocean caught and spawning eulachon was used to estimate age at maturation. Two size classes of eulachon were caught in the ocean and spawning eulachon were consistently the largest fish indicating that spawners from mid-coast of British Columbia were 3 years old. Laser-ablation inductively-coupled plasma mass spectrometry (LA-ICP-MS) was also used to reconstruct the Ba:Ca and Sr:Ca molar ratios deposited spatially into the otolith to estimate spawner age for five populations of eulachon. Age at maturation differed among populations examined. Based on the seasonal fluctuations in Ba:Ca molar ratios caused by seasonal upwelling of deep waters, it was determined that more southerly populations spawned at a younger age than the northern populations examined. Southern populations of eulachon, Columbia River, Washington, U.S.A., spawn after 2 years. Eulachon from the Fraser, Kemano and Skeena Rivers in British Columbia, Canada, generally mature after 3 years. Some Skeena River eulachon and most of the eulachon from the Copper River, Alaska, U.S.A., matured after 4 years. In contrast to the Ba:Ca molar ratios in the otolith, Sr:Ca molar ratios maintained a relatively flat profile over the life of the eulachon. The lack of a change in Sr:Ca ratios within the otolith, the single size class of spawners across all systems and the single age class within most populations strongly suggest that eulachon in the present study are semelparous.

© 2007 The Authors

Journal compilation © 2007 The Fisheries Society of the British Isles

Key words: anadromous; elemental ratios; eulachon; length; maturity; otolith.

### INTRODUCTION

The eulachon *Thaleichthys pacificus* (Richardson, 1836) is a small anadromous smelt that spawns from northern California to the southern Bering Sea. Populations

†Author to whom correspondence should be addressed at present address: Freshwater Fisheries Society of British Columbia, Fisheries Centre, 2202 Main Mall, University of British Columbia, Vancouver, BC, V6T 1Z4, Canada. Tel.: +1 604 222 6756; fax: +1 604 660 1849; email: [adrian.clarke@gofishbc.com](mailto:adrian.clarke@gofishbc.com)

of eulachon have shown a dramatic decline in numbers of spawners over much of their geographic range in the last 20 years. This trend has become particularly apparent since the mid-1990s and reasons for the decline are unknown. Information on the life history of eulachon is needed to determine what mechanisms are responsible for the observed declines. Two aspects of eulachon life history that are not known are age at maturity and the potential to repeat the spawning cycle.

Commonly, ages of fishes are determined by counting rings on bony structures such as otoliths. Estimates of age at maturity for eulachon are between 2 and 6 years (McHugh, 1939; Ricker *et al.*, 1954; Delacy & Batts, 1963; Hay & McCarter, 2000), but there is considerable controversy. Hay & McCarter (2000) suggest that age estimates from otoliths are unreliable for eulachon. An examination of the zonation in whole and transversely polished eulachon otoliths revealed problems encountered when interpreting age. Whole otoliths possess numerous dark bands or 'pseudo-annuli' that have been interpreted as winter growth zones in past ageing attempts. Additionally, sectioned otoliths viewed under transmitted light can reveal fewer zones that are difficult to interpret, suggesting that ageing by this method is problematic (Clarke, 2004).

Alternative methods to evaluate age, therefore, are needed for eulachon. Length-frequency relationships have been used in some fish species to determine age classes of fishes, but age classes of older and larger fishes commonly overlap and complementary techniques are needed to validate length-frequency methods to age fishes (McDowall, 1987). A method that may be appropriate for determining age at maturation for eulachon is seasonal oscillation in elemental signatures of bone. This procedure may corroborate the frequency of annuli formation, however, it must be kept in mind that elemental signatures may or may not fluctuate regularly or annually (Campana, 2001). There are a number of chemical signatures that have been consistently shown to have regular seasonal variation associated with fish migration or intra-seasonal variation due to temperature effects. Distinct chemical signatures have been found to vary in bony structures of saltwater fishes as a result of variable ion content (inshore and offshore), temperature and food sources and seasonal cycles in Na, Sr, K, S, Li, Mg and Ba (Elsdon & Gillanders, 2002; Bath Martin *et al.*, 2004) are often apparent.

Seasonal oscillations in Ba concentration are observed along the west coast of North America, so ageing eulachon otoliths using annual chemical oscillations may be a valid approach. Due to biological uptake, particle sinking, and then remineralization, Ba has a 'nutrient like' profile in the Pacific Ocean with concentrations that are three times higher in deep waters than in surface waters (Lea *et al.*, 1989; Nozaki, 2001; Esser & Volpe, 2002). From the surface to *c.* 400 m depth Ba concentration varies from 35 to 48 mmol kg<sup>-1</sup> and then rises to >120 mmol kg<sup>-1</sup> in water deeper than 1400 m (Chan *et al.*, 1976; Nozaki, 2001). On the other hand, Sr maintains a consistent concentration in both shallow and deep water (5740 m) with concentrations measured between 88 and 89 mmol kg<sup>-1</sup> (Chan *et al.*, 1976; Esser & Volpe, 2002). Summer upwelling events caused by seasonal winds (Eckman transport) cause Ba-rich deep waters to rise up and outcrop along the west coast of North America for *c.* 3 months each summer (Masson, 2002, 2006; Masson & Cummins, 2007). For eulachon rearing

along the coast of British Columbia, these upwelling events should therefore impart a seasonal Ba peak but a relatively flat Sr profile in their otoliths.

Length-frequency relationships have been used in some fish species to determine if fishes spawn more than once, but multiple age classes may overlap in size (McDowall, 1987). An alternate approach to determine multiple spawning events is to use the incorporation of elemental signatures in bony structures to assess movement patterns between spawning and rearing habitats. Different chemical signatures exist between marine and freshwater environments and these different signatures are incorporated into bony structures as fishes grow and move between these environments. Bony structures, therefore, provide a spatial elemental record corresponding to habitat use at each life stage of a specific population or individual. For this reason, elemental analysis of bony structures may reveal migration and movement patterns between fresh and sea water. Ca, Ba and Sr have been the most useful elements for this purpose. The objectives of this study were to test the value of using seasonal changes in elemental signatures to assess age and spatial changes due to the chemical differences between fresh and salt water to determine repeat spawning activity.

## MATERIALS AND METHODS

### FISH

Eulachon from five populations along the west coast of North America were sampled: the Columbia, Fraser, Kemano, Skeena and Copper Rivers and for ocean fish captured off the coast of Vancouver Island (Fig. 1). To describe eulachon size on the central coast of British Columbia,  $L_F$  data were obtained from two sources. Data on  $L_F$  in marine waters were provided by the Department of Fisheries and Oceans [these data are derived from analysis of eulachon by-catch in annual surveys of shrimp off the west coast of Vancouver Island, as described by Hay *et al.* (1999)]. Samples collected from Queen Charlotte Sound were compared to those collected in the Kemano River, which is located 130 km to the north. The Kemano  $L_F$  data were generated from samples collected from the Kemano River fishery conducted by the Haisla First Nation. This fishery uses seines to capture adult eulachon in the river during the spawning migration, harvesting *c.* 50% of the population. Samples of eulachon were collected from individual catches throughout the fishery and measured for  $L_S$  on-site by hand to the nearest mm.

Eulachon for elemental analysis were collected from the Skeena, Kemano, Fraser and Columbia Rivers between late January and May 2003, and from the Copper River in January 1998 and May 2001. In addition, eulachon were captured by a commercial shrimp trawler in July 2001 in Barkley Sound off the west coast of Vancouver Island, BC, Canada. The  $L_F$  (mm) and mass ( $M$ ; g) were measured for all fish and condition factor ( $K$ ) was calculated using the equation  $K = ML_F^{-3} \times 10^4$ . Both  $L_F$  and  $M$  were analysed with a one-way ANOVA and a Tukey's HSD *post hoc* test (SPSS v.11.5, Chicago, IL, U.S.A.). All data are presented as mean  $\pm$  s.e.

### SAMPLE PREPARATION AND DATA REDUCTION

In preparation for the elemental analysis, both the right and left sagittal otoliths were removed from 20 fish from each population and stored in plastic vials prior to returning to the laboratory. In the laboratory, otoliths were ultrasonically cleaned in ultrapure water for 5 min. Otoliths were then embedded in epoxy resin (Allied High Tech, Rancho Dominguez, CA, U.S.A.) and ground in the transverse plane with 1200  $\mu$ m silicon

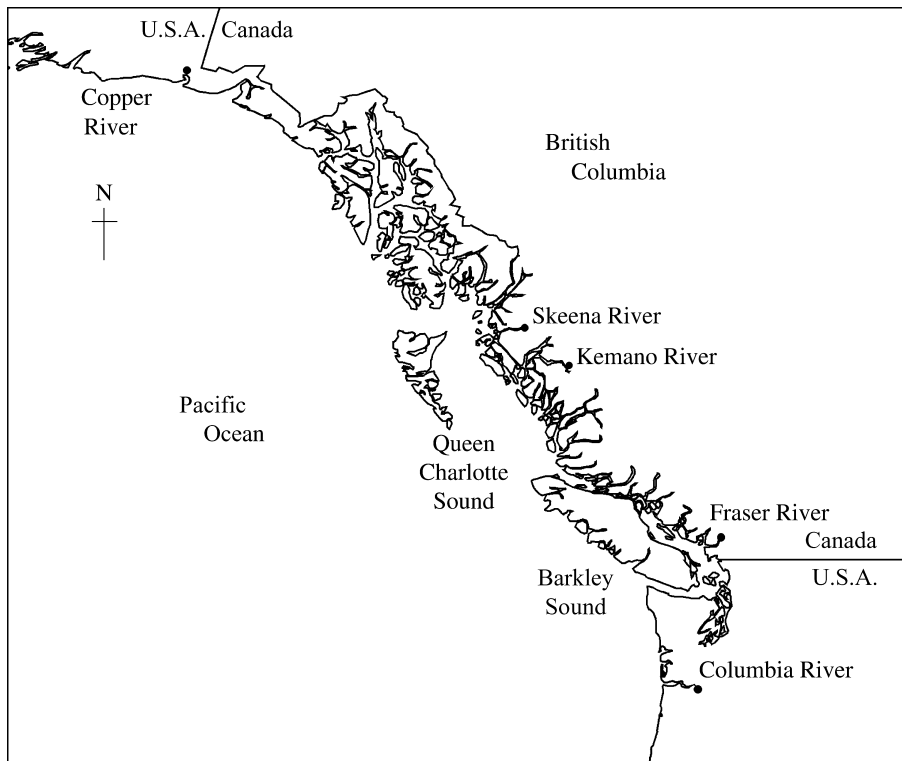


FIG. 1. Map of the Pacific coast of North America showing the locations of the five rivers where eulachon samples were collected and used in this study. Eulachon used for elemental analysis were also caught in the ocean, in Barkley Sound and fish for fork length-frequency analysis were caught in Queen Charlotte Sound.

carbide paper until the core was exposed. Wet grinding using ultra-pure water prevented external contamination of the samples. Otoliths were then sequentially polished with 6, 1 and finally 0.05  $\mu\text{m}$  diamond suspension to ensure an adequate surface for ablation with the laser. Otoliths were again ultrasonically cleaned in ultra-pure water for 5 min prior to analysis.

LA-ICP-MS analysis was conducted following the protocol outlined in Sanborn & Telmer (2003). Material was extracted from the otolith with a PQ II S+ high sensitivity ICP-MS (VG Elemental, Waltham, MA, U.S.A.) coupled to a UV laser ablation system (Merchantek, Fremont, CA, U.S.A.). The laser system operated with an output of 266 nm that has a maximum energy output of 4 mJ. Optimization was conducted using standard reference material (SRM) 613 NIST glass, containing *c.* 50  $\mu\text{g g}^{-1}$  total trace elements. All analyses were conducted at a frequency of 20 Hz with 75% power and the aperture of the laser set at one. Average energy while operating at these conditions was 0.70 mJ. The width of the laser scan was measured after analysis with a microscope mounted micrometer and was determined to be 25–32  $\mu\text{m}$ . Laser tracking across otoliths was completed at 5.3  $\mu\text{m s}^{-1}$ . The isotopes measured in the otoliths included  $^{43}\text{Ca}$ ,  $^{86}\text{Sr}$  and  $^{137}\text{Ba}$ . Ca was used as the internal standard due to the otoliths aragonite ( $\text{CaCO}_3$ ) composition. Ca is 40% of the molecular mass of aragonite. An internal standard was required to account for variations in aerosol production caused by the variation in the amount of material being extracted from the otolith by the laser. Background intensities were collected for 30 s prior to running the laser.

Data collection and reduction were completed using VG Thermo Electron Plasma-Lab Software 2003 (Version 1.06.007, Burlington, Ontario, Canada). Integration of the ICP counts was completed according to standard protocols (Sanborn & Telmer, 2003). The fully quantitative analysis option was chosen and an SRM 613 NIST glass was selected as the known standard. Two SRM 613 NIST glasses were analysed, both at the beginning and end of each run. These certified standards were used to complete an external drift correction to compensate for any changes in machine sensitivity. The precision for this method is  $\pm 3\%$  based on long-term internal laboratory data. Five otoliths were analysed between each set of standards. An SRM 611 NIST glass was also analysed as an unknown sample during each run of five otoliths to help ensure measurement accuracy and precision.

## RESULTS

The  $L_F$ -frequency relationships for eulachon captured in the marine environment and mature eulachon captured in the Kemano River for 2 year classes are shown in Fig. 2. The marine fish were captured in Queen Charlotte Sound, the closest marine area to the mouth of the Douglas Channel on the migration route to the Kemano River. Presumably, the larger size class of fish caught in Queen Charlotte Sound in 1999 would spawn in the Kemano River in

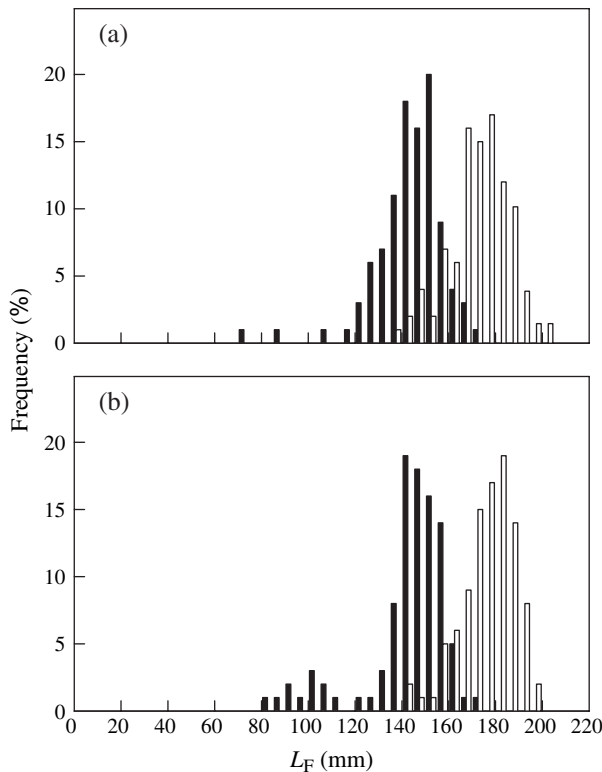


FIG. 2. Fork length ( $L_F$ )-frequency relationships for eulachon measured in (a) Queen Charlotte Sound (■) in 1999 ( $n = 184$ ) and in the Kemano River (□) in 2000 ( $n = 207$ ) and (b) Queen Charlotte Sound (■) in 2000 ( $n = 368$ ) and in Kemano River (□) in 2001 ( $n = 219$ ).

2000. The larger fish caught in Queen Charlotte Sound in 2000 probably spawned in the Kemano River in 2001. The 2000 Queen Charlotte Sound eulachon appear to have two size modes, suggesting two age classes; first- and second-year fish. Eulachon caught in the Kemano River in both 2000 and 2001 were consistently the larger fish and were probably a year older than fish caught in the ocean; this would indicate that spawners were 3 year-old fish.

The elemental profiles were similar for all of the eulachon populations examined. The elemental signatures determined for Sr:Ca are shown in Fig. 3. The profile for Sr:Ca remained relatively 'flat' over the life of all of the animals. There was no significant decrease in the Sr:Ca ratio near the core representing the larval fish or at the outer edge in association with the maturing fish returning to fresh water.

Ba:Ca ratios showed fluctuations that were quite consistent within populations. Ba:Ca ratio fluctuations across the otolith were found in all populations of eulachon examined (Fig. 4). All fish showed relatively high values at the core that decreased as the fish aged. After the initial decline, Ba:Ca ratios increased, showing an oscillating pattern with the number of oscillations differing among the populations (Fig. 4). Fish collected off the coast of Vancouver Island in July had the highest Ba:Ca values in the outer region of the otolith, whereas all fish caught in the spawning rivers during the winter and spring were characterized by low values of Ba:Ca in the outer region of the otolith. The outer region of the otolith represented the chemical environment the fish were exposed to near the time of sampling as the 30  $\mu\text{m}$  resolution attained in this study corresponded to *c.* 2 weeks of growth. The number of Ba:Ca peaks measured in the eulachon populations varied; eulachon captured in Barkley Sound, located off the west coast of Vancouver Island (ocean), had 1.5 and 2.5 peaks, Fraser River eulachon were all characterized by three peaks and Columbia River eulachon exhibited two or three peaks. All of the fish in the Kemano and Skeena Rivers examined were characterized by three peaks in Ba:Ca with the exception of two Skeena River fish that had four peaks. Fish collected from the Copper River in Alaska had three or four peaks. The number of peaks in Ba:Ca observed in eulachon otoliths increased with increasing latitude, suggesting that the age at maturity is older for northern populations.

The  $L_F$  of fish sampled compared to the number of peaks in Ba:Ca ratios for all otoliths analysed is shown in Fig. 5. The first decrease in Ba:Ca ratio is defined as the first peak (Fig. 4). This peak is probably not well defined as it represents the core of the otolith and due to the 30  $\mu\text{m}$  resolution the entire peak may not be resolved during ablation of the otolith. Eulachon caught in the ocean were the smallest, but all fish sampled from the rivers were similar in size (Table I and Fig. 5): >160 mm in  $L_F$  and >30 g. There was a significant difference in  $L_F$  for the populations examined ( $F_{4,193}$ ,  $P < 0.05$ ) and  $M$  ( $F_{4,193}$ ,  $P < 0.05$ ) among the mature samples collected from the five rivers. Tukey's HSD *post hoc* test revealed that there were significant differences among the populations. There was a trend towards larger fish in both  $L_F$  and  $M$  for more northerly populations and the largest fish were from Alaska and northern British Columbia (Table I). Although, there was a significant difference in  $K$  for the populations examined ( $F_{4,193}$ ,  $P < 0.05$ ), this same trend for  $L_F$  and  $M$  was not seen for  $K$ , where Kemano and Skeena River eulachon had the highest values for  $K$  (Table I).

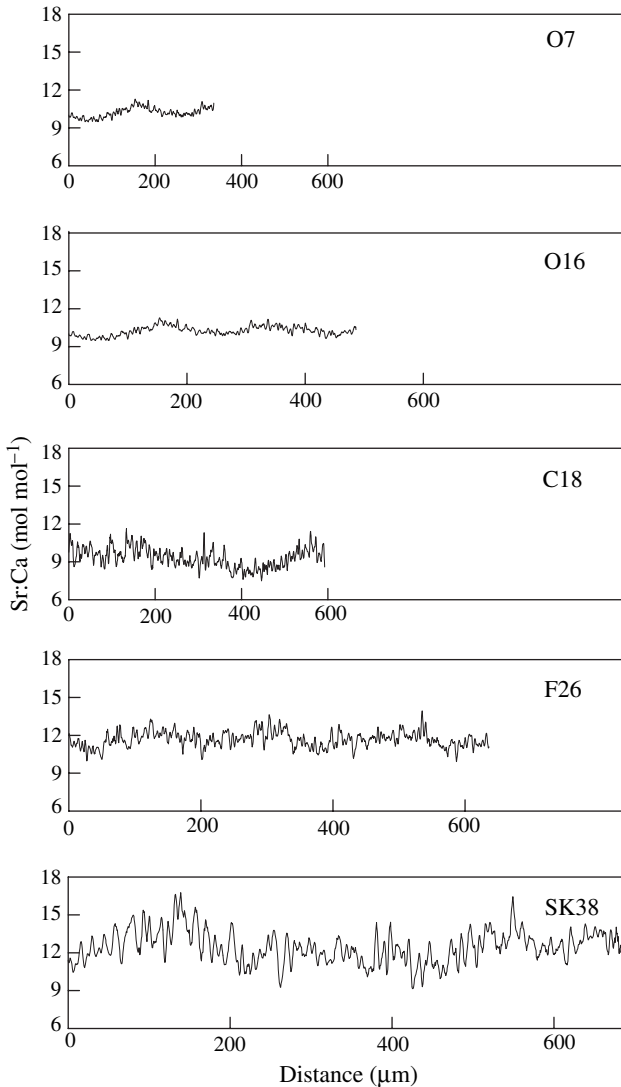


FIG. 3. Laser-ablation inductively-coupled plasma mass spectrometry line scans of Sr:Ca ratios for otoliths from four populations of eulachon showing relatively 'flat' transects. Fish O7 and O16 were captured off the west coast of Vancouver Island in Barkley Sound. Fish C18, F26 and SK38 were mature eulachon captured in the Columbia, Fraser and Skeena Rivers, respectively. Laser scan was initiated at the core and continued to the outer edge along the longest axis of the otolith. Size of otoliths at maturation was similar for all fish examined and was not related to age.

## DISCUSSION

### AGE AT MATURITY

Maturing fish in the Kemano River were estimated to be 3 years old. The age at maturity determined from the elemental analysis of the otoliths agrees with the  $L_F$ -frequency analysis of eulachon caught in Queen Charlotte Sound

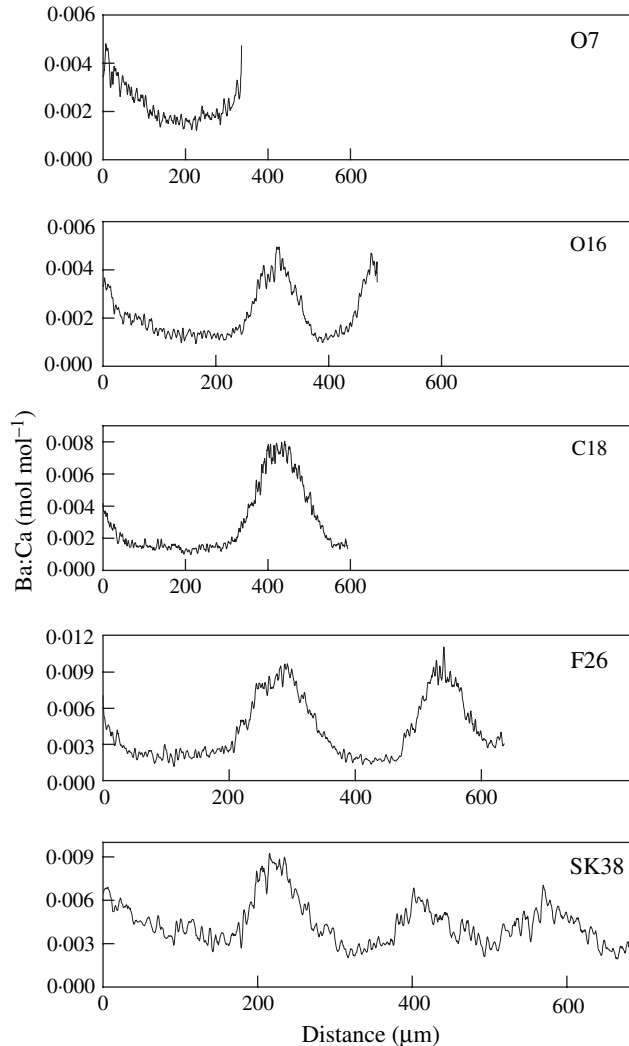


FIG. 4. Laser-ablation inductively-coupled plasma mass spectrometry line scans of Ba:Ca ratios for otoliths from four populations of eulachon showing different numbers of Ba peaks. Fish O7 and O16 were captured off the west coast of Vancouver Island in Barkley Sound. Fish C18, F26 and SK38 were mature eulachon captured in the Columbia, Fraser and Skeena Rivers, respectively. Laser scan was initiated at the core and continued to the outer edge along the longest axis of the otolith. Scaling on the distance axis was adjusted for each fish to line up the peaks in Ba. Size of otoliths at maturation was similar for all fish examined and was not related to age.

and the Kemano River (Fig. 2). Maturing fish appear to be composed of a single age class that is larger than any fish caught in the open ocean, suggesting that the mature fish caught in the river are at least a year older than the open ocean marine animals. Few fish from the younger age classes were captured in the ocean due to size selection of fishing gear, but a younger age class is seen in the 2000 Queen Charlotte Sound fish. Young-of-the-year fish were not captured, but the  $L_F$ -frequency data support an age at maturity estimate of 3 years



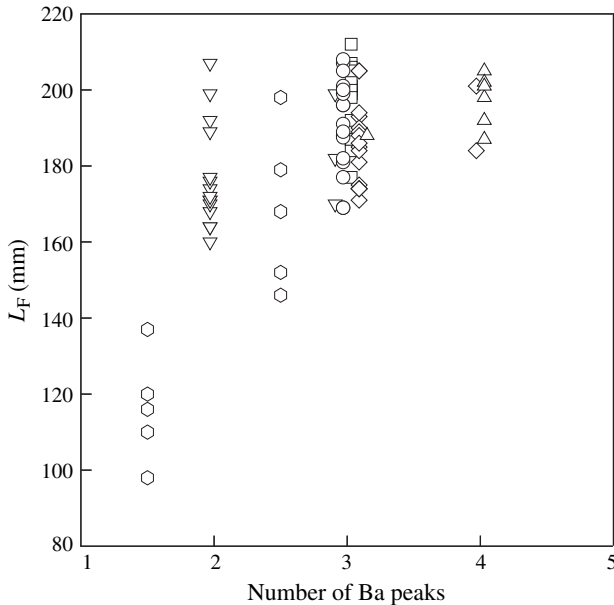


FIG. 5. The relationship between number of peaks in Ba:Ca elemental ratio and fork length ( $L_F$ ) of eulachon from the five river systems examined [Copper ( $\triangle$ ), Skeena ( $\diamond$ ), Kemano ( $\square$ ), Fraser ( $\circ$ ) and Columbia ( $\nabla$ )] and for ocean fish ( $\circ$ ) caught off the west coast of Vancouver Island.

for the Kemano River eulachon. The young-of-the-year age class has been captured in ichthyoplankton surveys conducted by the Department of Fisheries and Oceans Canada, and the  $L_F$  observed supports age estimates from the present study. During an 18–20 week period from April to August, 4 weeks after adult spawning, larval eulachon on average grow from 3–4 to 30–35 mm (McCarter & Hay, 1999).

Spawning eulachon in the present study were at least 160 mm  $L_F$  and >30 g, suggesting that eulachon spawn after reaching a minimum size. The age when fish reach the 160 mm threshold and mature varies with latitude: the Columbia River fish (the most southerly in latitude) spawn at the earliest ages, and the

TABLE I. Mean  $\pm$  s.e. fork length ( $L_F$ ), mass ( $M$ ), condition factor ( $K$ ) and age for eulachon captured from five river systems along the Pacific coast of North America. Values with a common superscript lower case letter do not differ significantly ( $P > 0.05$ )

River	$n$	$N$	$L_F$ (mm)	$M$ (g)	$K$	Age (years)
Columbia	25	18	175 $\pm$ 3 <sup>a</sup>	37.3 $\pm$ 1.8 <sup>a</sup>	0.68 $\pm$ 0.01 <sup>a</sup>	2.2 $\pm$ 0.1
Fraser	45	17	183 $\pm$ 3 <sup>b</sup>	47.2 $\pm$ 1.6 <sup>b</sup>	0.76 $\pm$ 0.01 <sup>b</sup>	3.0
Kemano	36	16	196 $\pm$ 3 <sup>c</sup>	57.5 $\pm$ 2.3 <sup>c</sup>	0.75 $\pm$ 0.01 <sup>b</sup>	3.0
Skeena	52	18	189 $\pm$ 2 <sup>b</sup>	48.7 $\pm$ 1.1 <sup>b</sup>	0.71 $\pm$ 0.01 <sup>a</sup>	3.1 $\pm$ 0.1
Copper	40	7	198 $\pm$ 1 <sup>c</sup>	55.4 $\pm$ 1.3 <sup>c</sup>	0.69 $\pm$ 0.01 <sup>a</sup>	3.9 $\pm$ 0.1

$n$ , sample size;  $N$ , sample size for laser-ablation inductively-coupled plasma mass spectrometry.

Copper River fish (most northerly river in latitude) spawn at the oldest ages (Fig. 5). Time to reach maturity may depend on environmental determinants of growth, such as temperature, requiring a longer time to reach size for maturation in more northerly populations. The very short freshwater residence time for eulachon suggests that the observed variation in age at maturation is due to latitudinal environmental differences in the marine environment. Findings for eulachon in this study are similar to results reported for another smelt and a species of Pacific salmon. The rainbow smelt *Osmerus mordax* (Mitchill, 1814) also shows considerable variation in age at maturity depending on environmental conditions. Rainbow smelt mature at age 2–4 years in Lake Huron (Frie & Spangler, 1985) and between 6 and 15 years in the Beaufort Sea (Haldorson & Craig, 1984). In an examination of age at maturity for chum salmon *Oncorhynchus keta* (Walbaum, 1792), it was found that maturity of slow-growing chum salmon was initiated at an older age than fast-growing chum salmon and that the fish examined demonstrated a phenotypic response to a reduced growth rate (Morita *et al.*, 2005). The authors felt that the most plausible explanation for the observed differences in age at maturation for chum salmon was environmental changes in the marine environment.

Fish captured in late July had high levels of Ba:Ca in the outer region of the otolith, characteristic of the maximum values measured in the otoliths. Conversely, fish captured between February and March had low Ba:Ca levels in the outer region of the otolith. The relationship suggests that eulachon otoliths are incorporating higher amounts of Ba during the summer *v.* the winter and that the oscillations correspond to seasonal variations. The high-summer–low-winter Ba levels in the otoliths also corresponds to the expected timing of ambient Ba concentrations in coastal waters, with summertime upwelling increasing Ba concentrations in surface waters. Using Ba variations to determine age, a single age class of fish was observed to spawn in the systems examined in this study. Only 3 year-old eulachon were observed from the spawning populations in the Fraser and Kemano Rivers, and the majority of fish for the Columbia, Skeena and Copper Rivers were also composed of a single age class; 2, 3 and 4 year olds from the Columbia, Skeena and Copper Rivers, respectively.

There are two possible explanations for the seasonal fluctuations observed: that the actual concentration of Ba:Ca fluctuates on a seasonal basis or that Ba:Ca incorporation is regulated by temperature dependent processes. Bath *et al.* (2000) demonstrated that Ba:Ca uptake into the aragonite matrix of the otolith is proportional to the concentration of Ba:Ca in the ambient environment. Because the concentration of Ba is approximately three times greater in deep Pacific Ocean water, summer upwelling events should reflect a proportional increase in Ba otolith concentration. The Ba:Ca values for eulachon in this study also showed approximately a three-fold change in magnitude, consistent with the magnitude of changes reported in the north-east Pacific Ocean.

An alternate explanation for the variation observed in Ba:Ca incorporation in eulachon otoliths could be that branchial (gill) uptake or chemical co-precipitation of Ba into aragonite is mediated by temperature-dependent processes. The degree of co-precipitation of any element is controlled thermodynamically by temperature, pressure and ambient chemistry. Elsdon & Gillanders (2002)

determined that the concentration ratio of Ba:Ca increased significantly in juvenile black bream *Acanthopagrus butcheri* (Munro, 1949) otoliths with increasing ambient water temperature. Sea-surface temperatures off the west coast of Vancouver Island follow a seasonal pattern with water temperatures around 7–8° C during the winter and spring and 12–14° C during the summer and autumn (McCarter & Hay, 2003). During the summer (June to September), when ocean temperature was highest, Ba:Ca deposition in the otolith was also highest.

The seasonal change in Ba:Ca levels observed in eulachon otoliths could be an additive effect of both summer upwelling events and differences in partitioning of Ba due to seasonal temperature changes. Summer upwelling events offer the least satisfactory explanation due to the support from the empirical chemical data: (1) known oceanography (summertime upwelling), (2) a clear proportionality between the magnitude of observed variations in otoliths (3×) and the magnitude of the known chemical variations in the ocean (3×), and (3) the lack of covariance with Sr; if temperature-induced co-precipitation were driving Ba variations, Sr would also be impacted (Townsend *et al.*, 1995) and therefore expected to vary with temperature along with Ba, but it did not. Further, the small interannual variations in Ba concentration in eulachon otoliths among years fit with upwelling. Summer upwelling events occur each year in the Pacific Ocean but depending on the weather, the degree of upwelling does change from year to year, which would induce yearly variability in surface water Ba concentration. Migration-induced signatures can be ruled out because the size of the Ba peaks is universal across populations separated by hundreds of kilometres. Finally, Sr:Ca ratios did not vary seasonally in eulachon otoliths, the profile was mainly flat throughout their life history, further supporting the summer upwelling hypothesis. Strontium concentration is much higher in sea water (*c.* 8 ppm) than Ba concentration (*c.* 0.015 ppm) and is evenly distributed throughout the water column so upwelling of deep waters does not induce a surface enrichment in Sr.

The seasonal fluctuations in Ba:Ca observed in this study suggests that, to date, many eulachon have been aged incorrectly. The use of seasonal variation in elemental signatures, therefore, represents an attractive alternative when ageing eulachon otoliths. Campana (2001) discussed the application of elemental and isotopic signatures for confirming the ages of growth structures assuming that the periodicity of growth increments would be accompanied by a periodicity in chemical composition. The problem with ageing eulachon using visible growth structure has come from identifying the specific increments in otoliths that correspond to annual zones. Eulachon otoliths possess frequent pseudo-annuli (visible increments formed by an unknown process), making ageing extremely difficult and resulting in a range of reported ages for mature eulachon (McHugh, 1939; Ricker *et al.*, 1954; Delacy & Batts, 1963; Hay & McCarter, 2000). The Ba:Ca variations appear to match expected annual shifts in ambient chemistry and so offer a more reliable annual marker for ageing.

## FATE AT MATURITY

The results indicate that eulachon are semelparous. The evidence for this conclusion is that the largest size class of eulachon found in the Kemano River

are spawners. If eulachon were iteroparous, fish as large as the spawners would also have been captured in the marine environment. The dominance of a single age class and single size class of fish observed spawning also strongly suggest that eulachon spawn only once. Finally, the similar size at maturity for each river system supports semelparity.

It was expected that the Sr:Ca profiles determined in this study would indicate movement of eulachon between fresh and sea water and indicate if these fish are semelparous. Sr:Ca ratios are significantly higher in the marine environment than the freshwater environment (Turekian, 1964). The Columbia, Fraser, Skeena and Kemano River watersheds are relatively dilute rivers with much lower Sr:Ca ratios than the ocean (Wadleigh *et al.*, 1985; Berner & Berner, 1996; Spence & Telmer, 2005). There have also been many studies indicating that migrations from fresh water to estuaries or the marine environment can be detected by high Sr:Ca ratios in bone, otoliths, scales and pectoral fin rays (Kalish, 1990; Coutant & Chen, 1993; Veinott *et al.*, 1999). Factors other than ambient concentration, however, also influence Sr:Ca ratios in some calcified structures. Seasonal changes in reproductive physiology have resulted in variations in Sr:Ca ratios (Kalish, 1991). In addition, temperature changes in the ambient environment have resulted in changes to the Sr:Ca ratios (Townsend *et al.*, 1989, 1995). The magnitude of the changes in Sr:Ca ratios when fish migrate from fresh to sea water, however, are so much greater than variations due to physiology or temperature. Sr:Ca ratios have been used to determine migrations into the ocean in Fraser River white sturgeon *Acipenser transmontanus*, Richardson, 1836, marine migrations (Veinott *et al.*, 1999) and anadromy in inconnu *Stenodus leucichthys* (Güldenstädt, 1772) from the Mackenzie River drainage (Howland & Tonn, 2001).

Surprisingly, although eulachon are known to spawn in fresh water, Sr signatures in eulachon do not reveal a freshwater signature. The lack of Sr variation in the otoliths of eulachon supports the hypothesis that they are semelparous. If a fish were iteroparous, then a decrease in Sr:Ca corresponding to time spent in fresh water would be expected at some time in the life history of the fish, but this was not evident. Although the 30  $\mu\text{m}$  resolution for the laser used to ablate these otoliths corresponds to *c.* 2 weeks of otolith growth, shorter term signals can still be detected; the magnitude of the change in concentration is less for short-term changes due to target mixing, but it is still clearly observable. This is known from the analysis of otoliths from chemical tagging experiments where fish are exposed to elevated Sr concentrations for just a few hours. In such analysis, a beam resolution of 50  $\mu\text{m}$  was able to clearly detect exposures of just 6 h (Telmer *et al.*, 2006). Material deposited onto the otolith just before death, however, is difficult to analyse because it is right at the edge of the target, and so a short end-of-life freshwater signal by the nature of its location in the otolith is difficult to observe. Eulachon migrate into river systems prior to spawning and have been reported to stay below the salt-wedge until just before spawning. Larval fish are also believed to spend little time in fresh water and are carried to the estuary soon after hatching (Hay & McCarter, 2000). The results, therefore, strongly support the idea that eulachon spend very little time in fresh water at either the beginning or end of their lives.

We would like to thank R. Cox of the School of Earth and Ocean Sciences at the University of Victoria for his assistance using the LA-ICP-MS. J. Zydlewski, Maine Cooperative Fish & Wildlife Research Unit, provided the Columbia River eulachon. D. Hay of the Pacific Biological Station provided the ocean samples and Fraser River samples. B. Marston, U.S. Fish & Wildlife Service, provided the samples from the Copper River in Alaska. We also thank B. McCarter of the Pacific Biological Station for helpful comments on an earlier draft of the manuscript. Finally, W. R. Crawford, Ocean Sciences Division, Institute of Ocean Sciences, Fisheries and Oceans Canada, gave us some useful information on summer upwelling off the coast of British Columbia. Financial support for this project came from the Kitsumkalum First Nation, Terrace British Columbia, Canada.

### References

- Bath, G. E., Thorrold, S. R., Jones, C. M., Campana, S. E., McLaren, J. W. & Lam, J. H. W. (2000). Strontium and barium uptake in aragonitic otoliths of marine fish. *Geochemica et Cosmochimica Acta* **64**, 1705–1714.
- Bath Martin, G. E., Thorrold, S. R. & Jones, C. M. (2004). Temperature and salinity effects on strontium incorporation in otoliths of larval spot (*Leiostomus xanthurus*). *Canadian Journal of Fisheries and Aquatic Sciences* **61**, 34–42.
- Berner, K. B. & Berner, R. A. (1996). *Global Environment, Water, Air, and Geochemical Cycles*. Upper Saddle River, NJ: Prentice Hall.
- Campana, S. E. (2001). Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation models. *Journal of Fish Biology* **59**, 197–242.
- Chan, L. H., Edmond, J. M., Stallard, R. F., Broecker, W. S., Chung, Y. C., Weiss, R. F. & Ku, T. L. (1976). Radium and barium at GEOSECS stations in the Atlantic and Pacific. *Earth Planetary Science Letters* **32**, 258–267.
- Clarke, A. D. (2004). Elemental signatures in bone to determine life history characteristics in fish. MSc Thesis, University of Northern British Columbia.
- Coutant, C. C. & Chen, C. H. (1993). Strontium microstructure in scales of freshwater and estuarine striped bass (*Morone saxatilis*) detected by laser ablation mass spectrometry. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 1318–1323.
- Delacy, A. C. & Batts, B. S. (1963). *Possible population heterogeneity in the Columbia River smelt*. Circular No. 198. Seattle, WA: Fisheries Research Institute, College of Fisheries, University of Washington.
- Elsdon, T. S. & Gillanders, B. M. (2002). Interactive effects of temperature and salinity on otolith chemistry: challenges for determining environmental histories of fish. *Canadian Journal of Fisheries and Aquatic Sciences* **59**, 1796–1808.
- Esser, B. K. & Volpe, A. M. (2002). At-sea high-resolution chemical mapping: extreme barium depletion in North Pacific surface water. *Marine Chemistry* **79**, 67–79.
- Frie, R. V. & Spangler, G. R. (1985). Dynamics of rainbow smelt during and after exploitation in South Bay, Lake Huron. *Transactions of the American Fisheries Society* **114**, 713–724.
- Haldorson, L. & Craig, P. (1984). Life history and ecology of a Pacific-Arctic population of rainbow smelt in coastal waters of the Beaufort Sea. *Transactions of the American Fisheries Society* **113**, 33–38.
- Howland, K. L. & Tonn, W. M. (2001). Identification of freshwater and anadromous inconnu in the Mackenzie River system by analysis of otoliths strontium. *Transactions of the American Fisheries Society* **130**, 725–731.
- Kalish, J. M. (1990). Use of otolith microchemistry to distinguish the progeny of sympatric anadromous and non-anadromous salmonids. *Fisheries Bulletin* **88**, 657–666.
- Kalish, J. M. (1991). Determinants of otolith chemistry: seasonal variation in the composition of blood plasma, endolymph and otoliths of bearded rock cod *Pseudophycis barbatus*. *Marine Ecology Progress Series* **74**, 137–159.

- Lea, D. W., Shen, G. T. & Boyle, E. A. (1989). Coralline barium records temporal variability in Equatorial Pacific upwelling. *Nature* **340**, 373–376.
- Masson, D. (2002). Deep water renewal in the Strait of Georgia. *Estuaries, Coastal and Shelf Science* **54**, 115–126.
- Masson, D. (2006). Seasonal water mass analysis for the Straits of Juan de Fuca and Georgia. *Atmosphere-Ocean* **44**, 1–15.
- Masson, D. & Cummins, P. F. (2007). Temperature trends and interannual variability in the Strait of Georgia. *Continental Shelf Research* **27**, 634–649.
- McCarter, P. B. & Hay, D. E. (2003). Eulachon embryonic egg and larval outdrift sampling manual for ocean and river surveys. *Canadian Technical Report of Fisheries and Aquatic Sciences* **2451**, 33pp.
- McDowall, R. M. (1987). The occurrence and distribution of diadromy among fishes. *American Fisheries Society Symposium* **1**, 1–13.
- McHugh, J. L. (1939). The eulachon. *Fisheries Research Board or Canada Pacific Progress Report* **40**, 17–22.
- Morita, K., Morita, S. H., Fukuwaka, M. & Matsuda, H. (2005). Rule of age and size at maturity of chum salmon (*Oncorhynchus keta*): implications of recent trends among *Oncorhynchus* spp. *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 2752–2759.
- Nozaki, Y. (2001). Elemental distribution. In *Encyclopedia of Ocean Sciences*, Vol. 2 (Steele, J. H., Thorpe, S. A. & Turekian, K. K., eds), pp. 840–845. San Diego, CA: Academic Press.
- Ricker, W. E., Manzer, D. F. & Neave, E. A. (1954). The Fraser River eulachon fishery, 1941–1953. *Fisheries Research Board of Canada Manuscript Report Biological Station, No. 583*.
- Sanborn, M. & Telmer, K. (2003). The spatial resolution of LA-ICP-MS line scans across heterogenous materials such as fish otoliths: an experiment on a sandwich of NIST glasses 611, 613, and 615. *Journal of Analytical Atomic Spectrometry* **18**, 1231–1238.
- Spence, J. & Telmer, K. (2005). The role of sulfur in chemical weathering and atmospheric CO<sub>2</sub> fluxes: evidence from major ions, delta C-13(DIC), and delta S-34(SO<sub>4</sub>) in rivers of the Canadian Cordillera. *Geochimica et Cosmochimica Acta* **69**, 5441–5458.
- Townsend, D. W., Radtke, R. L., Morrison, M. A. & Folsom, S. C. (1989). Recruitment implications of larval herring over wintering distributions in the Gulf of Maine, inferred using a new otolith technique. *Marine Ecology Progress Series* **55**, 1–13.
- Townsend, D. W., Radtke, R. L., Malone, D. P. & Wallinga, J. P. (1995). Use of otolith strontium: calcium ratios for hindcasting larval cod distributions relative to water masses on Georges Bank. *Marine Ecology Progress Series* **119**, 37–44.
- Turekian, K. K. (1964). The marine geochemistry of strontium. *Geochimica et Cosmochimica Acta* **28**, 1479–1496.
- Veinott, G., Northcote, T., Rosenau, M. & Evans, R. D. (1999). Concentrations of strontium in the pectoral fin rays of the white sturgeon (*Acipenser transmontanus*) by laser ablation sampling – inductively coupled plasma – mass spectrometry as an indicator of marine migrations. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 1981–1990.
- Wadleigh, M., Veizer, J. & Brooks, C. (1985). Strontium and its isotopes in Canadian Rivers – fluxes and global implications. *Geochimica et Cosmochimica Acta* **49**, 1727–1736.

### Electronic References

- Hay, D. E. & McCarter, P. B. (2000). Status of the eulachon *Thaleichthys pacificus* in Canada. *Canadian Stock Assessment Secretariat Research Document 145*. Available at: [http://www.dfo-mpo.gc.ca/csas/CSas/publications/ResDocs-DocRech/2000/2000\\_145\\_e.htm](http://www.dfo-mpo.gc.ca/csas/CSas/publications/ResDocs-DocRech/2000/2000_145_e.htm)
- Hay, D. E., Harbo, R., Boutillier, J., Wylie, E., Convey, L. & McCarter, P. B. (1999). Assessment of bycatch in the 1997 and 1998 shrimp trawl fisheries in British

- Columbia with an emphasis on eulachons. *Canadian Stock Assessment Secretariat Research Document 179*. Available at: [http://www.dfo-mpo.gc.ca/csas/Csas/publications/ResDocs-DocRech/1999/1999\\_179\\_e.htm](http://www.dfo-mpo.gc.ca/csas/Csas/publications/ResDocs-DocRech/1999/1999_179_e.htm)
- McCarter, P. B. & Hay, D. E. (1999). Distribution of spawning eulachon stocks in the central coast of British Columbia as indicated by larval surveys. *Canadian Stock Assessment Secretariat Research Document 177*. Available at: [http://www.dfo-mpo.gc.ca/csas/Csas/DocRech/1999/pdf/99\\_177e.pdf](http://www.dfo-mpo.gc.ca/csas/Csas/DocRech/1999/pdf/99_177e.pdf)
- Telmer, K., Penney, Z., Hamilton, A., Hume, J., Lofthouse, D. & Sheng, M. (2006). Strontium concentration profiles in reared juvenile sockeye salmon otoliths. *Transaction of the 13th Ocean Sciences Meeting, American Geophysical Union 87* (Supplement), Abstract 0S45J-12. Available at <http://www.agu.org/cgi-bin/SFgate/SFgate>