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Aspects of Sexual Maturation in Atlantic Salmon Suggested by Elemental Analysis of Otoliths and Gonadosomal Indices

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Abstract-We examined the maturity state of salmon caught in Newfoundland-Labrador fisheries during the period 1985-1988 and found that many fish believed to be on feeding migrations were in an advanced state of sexual development. To attempt to clarify the meaning of these data, chronological transects of strontium:calcium ratios from the otoliths of maturing and immature one seawinter fish were examined. Patterns of Sr:Ca ratio were not correlated with thermal, salinity, and somatic growth histories for all samples. Sr:Ca ratio in the freshwater portion of the otolith appeared to be influenced primarily by environmental strontium; whereas, ratios in the marine zone reflected sexual development. The ratios for immature fish suggested that an advanced state of sexual development was achieved during feeding migrations and that maturation regression occurred by late summer. Maturing fish were found to have Sr:Ca ratios similar to the immature fish of the same stock. The relative abundance of North American salmon that mature after two seawinters is correlated to the areal extent of over-wintering habitat in the Northwest Atlantic. A hypothesis is developed that relates the migration of post-smolts to this over-wintering area and their eventual maturation.

Introduction

Elements are often differentially deposited in the hard body parts of an organism during the chronology of its life. The first interpretations of the elemental history of biological samples were made for corals and assumed to represent the temperature regime the animal experienced during growth (Schneider and Smith 1982). Fish species contain a number of different hard body parts that have been scrutinized for elemental signals (Bagenal et al. 1973; Lapi and Mulligan 1981; Mulligan et al. 1983; Yamada et al. 1987; Coutant and Chen 1993): however, it has been the otoliths of fish that have yielded some of the most interesting results to date due to their resistance to chemical remodeling and stability during analysis (Campana and Neilson 1985; Gunn et al. 1992). A number of studies have ascribed interpretation of elemental signals in otoliths to environmental variables such as temperature and salinity (Kalish 1990; Radtke et al. 1990; Townsend et al. 1992). But, recent studies suggest that while physical parameters are important, physiological mechanisms and their concomitant seasonal cycles, such as growth and maturation, also influence chemical composition of otoliths (Kalish 1989, 1991; Gallahar and Kingsford 1992; Radtke and Shafer 1992; Sadovy and Severin 1992; Fowler et al. 1995; Fuiman and Hoff 1995). In the case of maturation, chemical composition of otoliths may reflect sexual development and spawning events and thus provide a record of the variation that occurs between individuals and populations. Otolith microchemistry may become an important tool in the study of maturation in fish populations (Gallahar and Kingsford 1992; Secor 1992).

The maturation mechanism in Atlantic salmon is complex and has important consequences on the generational contribution of gametes to a population (Saunders and Schom 1985; Myers 1986; Randall 1989). Though the physiology of maturation has been described (Rowe et al. 1991; Thorpe 1994), the influence and interaction of stock genetics (Saunders et al. 1983; Herbinger and Newkirk 1987), growth (Svedäng 1991; Thorpe 1994; Friedland and Haas 1996), and environmental factors (Martin and Mitchell 1985; Scarnecchia et al. 1989) on the proportion of a cohort that matures annually is still poorly understood.

Salmon populations in the Northwest Atlantic exhibit maturation schedules that produce runs of predominately one seawinter (1SW) or 2SW salmon (Power 1981; Saunders 1981). Post-smolts of these populations migrate from a wide latitudinal range and are found feeding as far north as the Labrador Sea after only a couple months in the marine environment (Reddin and Short 1991). Most post-smolts are presumed to overwinter in the vicinity of the Grand Banks, likely moving into this area in response to changes in water temperature and the food availability (Reddin 1985; Reddin and Friedland 1993). After the overwintering period, some 1SW fish return to natal rivers to spawn. However, other 1SW fish migrate to feeding areas in the Labrador Sea and are concentrated along the Newfoundland and Greenland coasts (Møller Jensen 1990; May 1993). These salmon do not mature until the following year.

Salmon destined to sexually mature are believed to undergo physiological changes that differentiate them from the immature component of the cohort (Thorpe 1988). It is also believed that the marine homing behaviors of maturing salmon are maturation specific since the homing ability is so precise (Hansen et al. 1993). Ultimately therefore, the process of sexual maturation

and the return migration are intimately linked.

In this paper, we present observations of the age and apparent maturation state of salmon migrating along the Newfoundland-Labrador coast during summer. We then compare the otolith Sr:Ca ratios for maturing and immature 1SW salmon on spawning and feeding migrations, respectively. These two sets of observations are found to be complementary and form the basis for a discussion of migration and maturation mechanisms in Atlantic salmon.

Materials and Methods

State of Maturity of Salmon Migrating in Canada

Discriminant analysis of gonadosomatic indices (GSI) was used to determine the maturity state of salmon caught in the commercial fisheries of Newfoundland and Labrador. The technique required samples of salmon of known and unknown maturity. The known maturity sample was used to develop a discriminant analysis model and test its basic assumptions. After the model was formulated and evaluated, data for fish of unknown maturity state were classified. The indicator variable used in the discriminant analysis was GSI and was calculated for each fish as follows:

GSI = gonad weight / whole weight;

where whole weight was measured to the nearest gram and gonad weight was measured to the nearest 0.1g. Discriminant models were developed separately for male and female salmon.

The sample of known maturity salmon consisted of immature 1SW fish taken in research vessel gillnet catches in the Labrador Sea each fall during 1987-1989 (Reddin and Short 1991) and maturing 1SW salmon taken in gillnets and by anglers in the Conne River, Newfoundland (Reddin and Short 1986). Gonad and whole weight measurements were taken from all fish. Cross-validation results yielded a misclassification rate of 4.7% and an error rate of ±0.7% for male salmon, and a misclassification rate of 7.7% and error rate of ±1.1 for female salmon (Table 1).

Maturity samples of salmon in the commercial fishery were taken from commercial landings at Twillingate, Newfoundland, and Square Islands, Labrador during 1985-1988 (Figure 1). Samples consisted of scales for aging, whole weight, and gonad weight obtained daily from the commercial landing sites. A total of 3,077 fish were analyzed, 1,856 of which were males and 1,221 females.

Elemental Analysis of Salmon Otoliths

Atlantic salmon otoliths used for elemental analysis were collected from 28 immature and 13 maturing salmon (Table 2). Immature fish were sampled from commercial catches at West

Greenland during 1987 and 1988. Nineteen of these fish were tagged with coded-wire tags as juveniles, thus providing river and continent of origin (Table 2). The nine other immature fish were of unknown origin and assumed to be a mixture of wild stocks originating from both North America and Europe. All fish at Greenland were immature 1SW salmon and thus would not have spawned until the following year. Thirteen maturing fish were sampled from traps in two US rivers in 1994 and 1995. A sample of eleven 1SW spawners were taken from the Penobscot River and two 2SW spawners were collected from the Merrimack River. A sample of 10 smolt otoliths was also taken from fish in the Penobscot River in 1994 for morphological measurements only (i.e. not included in Table 2). In all samples, the sagittal otoliths were extracted and stored dry in envelopes or vials.

Secondary ion beam mass spectrometry was used to determine the concentrations of Ca and Sr in chronologically ordered locations in sagittal otolith hemisections. Otoliths were prepared for analysis by cleaning them with water and rinsing with ethanol. Once dry, the otoliths were embedded in epoxide resin, cured, and the resin blocks cut transversely through the otolith focus with a low speed saw. The posterior sections were then embedded in aluminum rings for polishing. Otolith surfaces were leveled using 800 grit paper, followed by 1200 grit paper on a lapping wheel, and then cleaned in an ultrasonic cleaner. The otoliths were polished on nylon mesh with 5.0 micron alumina, followed by 1.0 and 0.3 micron alumina on a wet microcloth with ultrasonic clearings in between. After wiping with ethyl alcohol, the samples were stored under vacuum. Preparation for mass spectrometry analysis was completed by sputter coating the samples with gold at a thickness of approximately 300 Å.

A Cameca IMS 3f ion microprobe was used to measure secondary ion intensities of ^{40}Ca and ^{88}Sr. A primary beam of O^- ions was used with a net energy of 12.61 keV and an ion current of ~1 nA, focused to a spot of approximately 5-8μm in diameter. The secondary positive ions released from the bombardment were accelerated to 4.41 keV and analyzed with combined electrostatic and magnetic analyzer sectors. Secondary ions were detected with a 17 stage Allen type multiplier in pulse counting mode with a pulse amplifier/discriminator following TTL pulse counting. The energy bandwidth of the secondary ion analyzer was adjusted to ±10eV.

Secondary ion intensities were measured on peak top intensities for ^{40}Ca and ^{88}Sr. For each analysis, 5 measurement cycles were made and an average intensity ratio against Ca was calculated based on 4 sets of doubly time-interpolated ratios. The coefficient of variation for Sr:Ca measurements was typically less than a percent; thus, confidence intervals were not plotted on the figures since intervals would not exceed the dimensions of the point estimate markers.

Ion counts were collected from a standardized transect of the otolith hemisection. First, a point on the proximal surface of the otolith (point C in Figure 2A) was located midway between the dorsal tip (point A) and the dorsal edge of the sucul grove (Point B). The line between Point C and the focus (Point D) represented the standard transect. However, it was not possible to take all samples along the standard transect due to an inability to accurately locate points and the desire to avoid surface imperfections on the polished otolith. While measurements were being

made, vatteritic otoliths were identified by both morphology and ion counts; these sample were then excluded from the study.

After the ion counts were completed, computer image processing was used to determine the positions of sample locations along the standard hemisection transect. Using reflected light optics, an image was captured that showed the surface topology of the otolith and the position of ion beam burn spots. The distance from the otolith focus to a site along the standard transect having the same chronology as a burn spot was determined using the topology of the otolith ring structure (Figure 2B). These distances, in millimeters, are referred to as standard positions and were used to facilitate comparisons among otoliths. However, standard positions were not equivalent among samples due to the different growth rates among individuals, unequal hemisections, and measurement error. The average total length of the standard transect from a sample of 10 smolts (average=0.54 mm) was used as an indication of the demarcation between freshwater and marine zones of the otolith.

Comparison of Growth and Elemental Deposition

Marine growth was characterized by measuring the circuli spacing on scales. Circuli spacing was measured from the end of the freshwater zone of the scale to the outer edge. The spacing reflects growth during the post-smolt year and through the 1SW summer when the fish were caught. Scales were prepared and circuli spacing measured following the methods of Friedland and Haas (1996) with the exception that four additional measurements were made over approximately a 15° sector of the scale centered on the 360° axis of the scale. The five independent measurements of circuli spacing were averaged by circuli pair and standard deviations computed.

Circuli spacing growth patterns were compared to patterns of Sr:Ca ratio in the otolith by plotting both data sets over standardized chronologies. For the circuli spacing data, the standardized chronology was the distance from the beginning of the marine zone divided by the distance to the edge of the scale. Thus, the first circuli spacing occurred at standardized chronology 0.0 and the last circuli spacing at standardized chronology 1.0. The standardized chronology for the Sr:Ca ratios were computed in a similar manner except that measurements less than 0.54 mm from the otolith focus were assumed to be from the freshwater zone and thus excluded. Hence, the standardized chronology was computed by first subtracting 0.54 mm from each standardized position, and then dividing by the new value for the outer edge position.

Results

State of Maturity of Salmon Migrating in Canada

Maturation rates of salmon caught in the Newfoundland and Labrador commercial fisheries ranged from a low of 43% for female, river age 2 salmon to a high of 100% for male, river age 6 fish (Figure 3). Though the dates varied over the sampling period, the spring fishery

generally peaked by late June and was completed within a few weeks. The maturation rates of river age 1 and 2 salmon were surprisingly high because most of these fish are thought to be destined to spawn in rivers south of Newfoundland the following year. As marked in Figure 1, rivers tending to produce river age 2 salmon are well to the south of the sampling sites; thus, the feeding migration along the Newfoundland and Labrador coasts would take the fish in a northwesterly direction away from these rivers (Figure 1). The river age 1 fish caught in the Newfoundland-Labrador fisheries were from hatchery programs in Nova Scotia and the northeast United States and unlikely to spawn until the following year.

Elemental Analysis of Salmon Otoliths

Strontium:calcium ratios in salmon otoliths varied chronologically and systematically in patterns common to all individuals. Overall, Sr:Ca ratios ranged from a low value of 0.00008 to a high of 0.00281 (Table 3). We found it convenient to consider Ca:Sr ratios deposited during the freshwater phase separately from those deposited during the marine phase. Using the standard position of 0.54 mm as an approximate demarcation between freshwater and ocean life, ratios in the freshwater region were generally about 0.001 whereas ratios during the marine phase followed a consistent pattern of increasing to levels in excess of 0.002. Freshwater ratios were more variable than those from the marine zone as indicated by the coefficients of variation of minima and maxima from the two zones (Table 3).

Freshwater Sr:Ca ratios for fish captured at West Greenland tended to vary by stock origin. Freshwater ratios for North American hatchery fish ranged from 0.00044 to 0.00139 (Table 3); however, since most North American specimens were from hatchery fish we saw little within sample variability (Figure 4A). Ratio values in the freshwater zone of European origin fish ranged from 0.00008 to 0.00217 (Table 3) and also generally showed little ontogenetic pattern in this region of otolith, but there were some exceptions (Figure 4B). Specimen A3 had the highest freshwater Sr:Ca ratios of all samples and was also of wild origin.

Marine Sr:Ca ratios for immature 1SW fish captured at West Greenland followed a pattern of monotonic increase to a peak level followed by a decrease before the fish was captured. Regardless of stock origin and freshwater Sr:Ca ratio levels, when these fish entered the marine environment the Sr:Ca ratios converged to a level of approximately 0.0015 and gradually rose during the period of post-smolt growth (Figure 4A and 4B). Maximum values of the ratio were generally between 0.0020 and 0.0025. Another feature of the Sr:Ca ratio curves for immature salmon was the decline in the ratio before the fish was captured in late summer to early fall. Strontium deposition was clearly higher for these animals during either the summer or spring period before their capture.

The Sr:Ca ratios for the eleven maturing 1SW fish taken from the Penobscot River displayed two general patterns of Sr:Ca ratio values during their marine life. During the early phase of their marine life Sr:Ca ratios were approximately 0.0015 and then increased to about 0.002 throughout the remainder of their marine residency (Figure 5). About half the samples

showed a distinct peak in Sr:Ca ratio immediately prior to entry into their natal river (Figure 5A), whereas the balance showed little evidence that the ratio ever peaked before capture (Figure 5B). The overall extent of this phenomenon can be seen by differencing the maximum Sr:Ca ratio observed in the marine zone and the ratio observed near the edge of the otolith (Table 3). These differenced values were positive for the fish taken in Greenland whereas for many maturing fish the difference is very low.

Sr:Ca ratio decreases after the first sea summer but increases again before spawning in maturing 2SW fish returning to the Merrimack river. The chronology of Sr:Ca for a female spawner can be seen in Figure 6A. After the first peak in Sr:Ca ratio, which appears in a position similar to that observed in fish captured in Greenland, the ratios decline to less than 0.002. The second peak occurs in the year after the second sea winter at sea. A nearly identical pattern was observed for the male 2SW fish (Figure 6B). Both salmon were spawned and held in a hatchery an additional month before being sacrificed: this may explain the decline in Sr:Ca after the second peak. The freshwater zones for these fish showed relatively little fluctuation in Sr:Ca ratio; however, there is evidence of a minor peak associated with standard position 0.4mm. Both of these fish were stocked as fry and thus spent their juvenile residence in the river as opposed to a hatchery.

Marine Sr:Ca ratios for maturing and immature Penobscot River salmon were nearly identical. We plotted the Sr:Ca ratios for Penobscot fish in Figure 7 and limit the range of the standardized position to 0.6 mm and above to minimize the risk of including any values from otolith material deposited during freshwater residency. The ratios are similar for the two maturity groups as suggested by the overlap of the 95% confidence intervals of polynomial regressions. We discount the divergence of the high end of the regressions at the greater standardized positions since the mean standardized transect length of the maturing fish was much less than for the immature fish. The same data for the Penobscot immature fish was also compared to ratios from a mixture of immature, wild salmon of unknown stock origin. The ratios for the nine, 1SW wild origin fish were apparently higher than for the Penobscot stock (Figure 8).

Comparison of Growth and Elemental Deposition

The chronology of marine growth as evidenced by circuli spacing patterns was similar for all samples. The beginning of the chronology was characterized by rapid growth rate associated with the first summer at sea for both maturing and immature examples plotted (Figure 9). This was followed by a period of slow growth which is the winter period and then followed by rapid growth again which is the second sea summer. In maturing fish, there is evidence that growth is arrested at the end of the chronology (Figures 9A and 9B). However, growth remained at a high level right up until capture for immature fish (Figures 9C and 9D). The Sr:Ca ratios for the same fish followed different chronological patterns. Sr:Ca ratios are at their lowest values at the beginning of the chronology when growth rate is rapid; however, when growth rate returned to these high levels during the second sea summer, Sr:Ca generally remained elevated. In addition,

the winter growth reversal evidenced on the scales is a feature lacking from the Sr:Ca time series.

Discussion

The Sr:Ca ratios of Atlantic salmon otoliths appear to be a record of sexual development and maturation. This hypothesis is based on our own observations and emerging research that correlates strontium deposition patterns to physiologic ontogeny (Kalish 1989, 1991; Gallahar and Kingsford 1992; Sadovy and Severin 1992; Fuiman and Hoff 1995). As recommended by Fowler et al. (1995) each species should be examined on a case by case basis to determine the mechanisms controlling the incorporation of chemical constituents into body hard parts. We were able to evaluate environmental levels of strontium, temperature, salinity, and somatic growth as the strontium controlling mechanisms by considering the freshwater and marine regions of the otolith and by correlation with known histories for individual otoliths.

The Sr:Ca ratio chronologies we observed in the freshwater regions of salmon otoliths usually had little contrast within individuals; however, the overall levels of Sr:Ca ratio varied greatly among the various stock groups studied. Chemical constituent differences among various watersheds has been one of the features used in stock identification research with anadromous species (Mulligan et al. 1987). This is due to the water chemistry differences among various river systems, which contrasts open ocean strontium availability which is relatively constant and generally higher than in freshwater. This environmental plasticity in strontium deposition in otoliths is also reflected in how strontium levels are manipulated for use as a chemical mark in experimental research (Schroder et al. 1995). Therefore, we believe that freshwater Sr:Ca ratios were primarily influenced by the level of environmental strontium.

The effect of water temperature on Sr:Ca ratio was evaluated by considering the Sr:Ca chronologies from fish that were resident in freshwater for multiple years and by contrasting ratio levels in freshwater versus the ocean zone of the otolith. Temperature has been convincingly related to strontium deposition in otoliths for a number of species (Gauldie et al. 1986; Radtke 1989; Townsend et al. 1992). From these studies, there appears to be a negative relationship between temperature and Sr:Ca ratio when other factors are controlled. The 2SW spawners from the Merrimack River were resident in freshwater for two years and thus experienced, at a minimum, a yearly 20°C excursion in water temperature while resident in freshwater streams. This is based on the assumption that water temperature during winter would approach 0°C and could easily exceed 20°C during summer. These temperature changes are not reflected in the freshwater Sr:Ca ratios observed for these fish. Furthermore, the ocean temperature that the fish would have experienced would fall within the freshwater temperature range with an upper temperature likely lower than 20°C (Reddin and Friedland 1993), yet all marine Sr:Ca ratios for the fish are above those observed for freshwater.

As has been demonstrated for salmonids and clupeids (Kalish 1990; Limburg 1995, Secor et al. 1995) salinity affects the concentration of strontium in otoliths. We observed wide variation in the Sr:Ca ratio in the freshwater region of the otoliths, a period during which all juveniles

would have been in 0‰ salinity waters with the exception of some pre-smolt migrants which may have utilized the estuary before migrating (Cunjak et al. 1990). Therefore, if salinity is the principal factor determining Sr:Ca ratios in salmon, one would expect to see all the fish start at nearly the same ratio level; and, perhaps some wild origin fish have increasing Sr:Ca in the section of the otolith considered to be the later part of the freshwater phase. However, this was not observed; instead, individual stocks tended to have specific ratio levels associated with them. Undoubtedly, differences in water chemistry or pollution loading, not salinity, must have caused these differences. Furthermore, salmon migrate to sea very rapidly, going from freshwater to ocean salinities in a matter of weeks (Mills 1989). The Sr:Ca ratio chronologies observed in the salmon we sampled had no discontinuity around the region of the otolith that would have been laid down during that transition; instead, the increase in Sr:Ca ratio was gradual. Water chemistry, therefore, must play a significant role in influencing Sr:Ca ratio levels in freshwater, but in the marine environment, where environmental strontium levels are less variable, otolith concentration are clearly influenced by other factors.

The monotonic increase in Sr:Ca ratio during the first half of the marine phase suggests that strontium incorporation was related to growth since the post-smolt year is a period of rapid and sustained growth for salmon (Gauldie et al. 1995; Halden et al. 1995). However we see little similarity between the growth history suggested by the circuli spacing data (Doyle et al. 1987; Barber and Walker 1988; Fisher and Pearcy 1990) and the Sr:Ca chronologies for individual fish, suggesting that some other physiologic mechanism is responsible. Work by Fuiman and Hoff (1995) suggests that other isotopes may be more responsive to physiologic changes in fishes during annual reproductive cycles and that strontium deposition generally increases with age and maturity of the fish. The experimental work of Kalish (1991) explicitly showed that strontium levels in otolith endolymph are related to the presence of metal binding proteins associated with seasonal reproductive cycles. Sr:Ca increased during the post-smolt year and peaked at or immediately before maturation for 1SW salmon and peaked a second time in fish maturing at age 2SW. We found the marine patterns of Sr:Ca ratios in salmon to be consistent with what is known of the maturation process in salmon: thus, we suggest that the Sr:Ca ratio serves as an indicator of reproductive state in Atlantic salmon. This view is further supported in the literature by Kalish (1989), Rieman et al. (1994), and Gallahar and Kingsford (1996).

The marine Sr:Ca ratios for salmon captured at West Greenland suggest that these fish were in a state of maturation regression when captured and were at some higher level of sexual development during the months prior to the fishery. This observation puts observations of GSI indices in Canada into perspective suggesting that fish captured in Canada, which were taken earlier in the summer, were actually in a more advanced state of sexual development. Thus, river age 1 and 2 salmon, which are non-native to the Newfoundland coast and would be unlikely to mature that season, were found to be maturing. The data from Greenland suggest that at least some of these fish may have also regressed had they survived to migrate to northern Labrador later in the year. Salmon studied in the laboratory can show evidence of early sexual maturation as measured in peripheral steroid hormone levels, rather than pituitary or hypothamalic activity that precedes gonad activity, and still not mature in the current cycle (Hunt et al., 1982;

Youngson et al., 1988; McLay et al., 1992). In other words, these fish begin to mature and then regress, which would parallel the phenomenon we observed in nature. Furthermore, our observations with 2SW spawners suggest this level may continue to decline into the fall which explains why those 1SW fish captured in the Labrador Sea during fall and used to calibrate the GSI discriminant function clearly presented as immature salmon. A different pattern may have emerged if the same fish were sampled earlier in the year.

When the elemental patterns for immature fish was compared to those for mature fish of the same sea-age and stock, i.e. the Penobscot River stock, we saw nothing to suggest that the mature fish were in a more advanced reproductive state than immature fish captured in Greenland. The Sr:Ca ratios suggest the two maturity groups are on similar maturation trajectories and that these trajectories may vary by stock. Neighboring stocks can often have widely different survival and maturation schedules (Friedland 1995); thus, the observation that other stocks at West Greenland have different Sr:Ca ratios than observed for the Penobscot shows that the ratios vary as a function of stock. However, the results within stock are surprising. We would expect a more demonstrable divergence in the development of fish destined to mature after the first seawinter versus those that are not. Though the data are not conclusive, it appears that some component of the maturation process is related to the influence of the post-smolt migration and that maturation may not solely be the result of a series of physiological-behavioral mechanisms.

This leads us to propose a hypothesis that migration may be a significant determinant of maturation in salmon, which we support with data on the relationship between population abundance trends and ocean climate. Though we specify the hypothesis for southern North American salmon stocks, ones with age structures that include fish that mature at both 1SW and 2SW ages, we suspect it can be generalized. The principal aspect of the hypothesis is that fish that migrate more northerly as post-smolts are differentially affected by overwintering conditions and may also find themselves in a location after winter where they fail to receive cues related to sensing their home rivers. Thus, these fish feed and grow and join feeding migrations into the Labrador Sea. As a consequence, they regress in their maturation state. Alternatively, fish that make a more southerly post-smolt migration experience different overwintering conditions and are closer to home rivers after winter. They are more likely to receive cues associated with their natal rivers, develop sexually, and invoke other behaviors to navigate home. This segment of the salmon's migration is not well known; however, it is clear that homing salmon change behavior in response to cues associated with natal rivers (Hansen et al. 1993). Though not well studied, there is precedence for relating migration to maturity. Woodhead (1959) found that immature cod in the Barents Sea following different migration routes showed differing patterns of sexual development.

What clearly elevates this idea from pure speculation is the fact that the abundance of North American 2SW spawners is correlated with the areal extent of thermal habitat during their first seawinter. This relationship remains unexplained, however, proponents of the relationship have always been uncomfortable with the idea that this abundance is determined by a mortality

effect during the winter season (Friedland et al. 1993). If on the other hand, the ocean climate simply influences a segment of the stock to take a more northerly post-smolt migration and thus not mature after the first seawinter, both sets of phenomena would be explained.

This hypothesis would predict that salmon stocks originating from rivers located in the feeding areas would have high 1SW maturation rates. Because these stocks are already in the northerly end of the range, their post-smolts would be unlikely to migrate south and their feeding migration would take them past natal rivers, thus insuring potential 1SW spawners are exposed to cues that may elevate pre-spawning behaviors. This is generally true for stocks in Newfoundland and Labrador which tend to produce dominant grilse runs compared to more southerly North American rivers (Power 1981; Saunders 1981).

We assume that older fish have more developed secondary sexual characteristics and thus the likelihood of returning to their natal river is less affected by their migration and distribution. Salmon stocks achieve high reproductive fitness by returning after 2SW in age and before the accumulated effects of natural mortality on older sea-ages. The locating of the home river is in achieved by changing thermal preferences and by navigational mechanisms that are still being actively debated (Dittman and Quinn 1996). The low number of salmon returning to North American rivers after three or more seawinters suggests that physiologic changes related ot homing become more effective after the second seawinter.

The role of growth in achieving maturation becomes less clear in light of this hypothesis. Friedland and Haas (1996) recently reported that the fraction of a cohort that matures annually was correlated with summer growth. This finding was supported by an analysis of two stocks with widely different growth, survival and maturation rates (Friedland et al. 1996). However, these conclusions were based on trends in returns of various aged fish and not an examination of the physiology of individual animals. An apparent increase in the return of 1SW salmon, interpreted as a tendency to mature early, could also be a reflection of improved survival with better growth. Of probably greater relevance was the finding of Friedland and Haas (1996) that only winter growth differed systematically between 1SW and 2SW fish of the same stock and cohort. Winter growth rate was found to be higher in 1SW fish which is consistent with the notion that fish destined to mature at 1SW were in a different location and experienced different conditions during the first seawinter. However, part of the maturation process may be independent of growth and the proportion of the cohort surviving if there is an environmental effect on migration. Clearly there are minimum growth requirements for salmon to mature and these generally conform to the evolutionary patterns observed for teleosts (Stearns and Crandall 1984; Stearns 1992). We therefore argue that maturation in salmon is influenced by growth rate, but also argue that an environmental mechanism exists that facilitates migration to areas that favor differing maturity patterns.

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Table 1. Cross-validation summary using quadratic discriminant function for determining stage of maturity of male and female salmon.

Males		Observed		
		Mature	Immature	Total
Predicted	Mature	55	4	59
	%	*93*	*7*	*100*
	Immature	3	86	89
	%	*3*	*97*	*100*
	Total	58	90	148
	%	*39*	*61*	*100*
Misclassification Rate: 4.7%				
Error Rate: ±0.7%				

Females		Observed		
		Mature	Immature	Total
Predicted	Mature	209	18	227
	%	*92*	*8*	*100*
	Immature	24	291	315
	%	*8*	*92*	*100*
	Total	233	309	542
	%	*43*	*57*	*100*
Misclassification Rate: 7.7%				
Error Rate: ±1.1%				

Table 2. Sample information for otoliths used in analysis of Sr:Ca ratios.

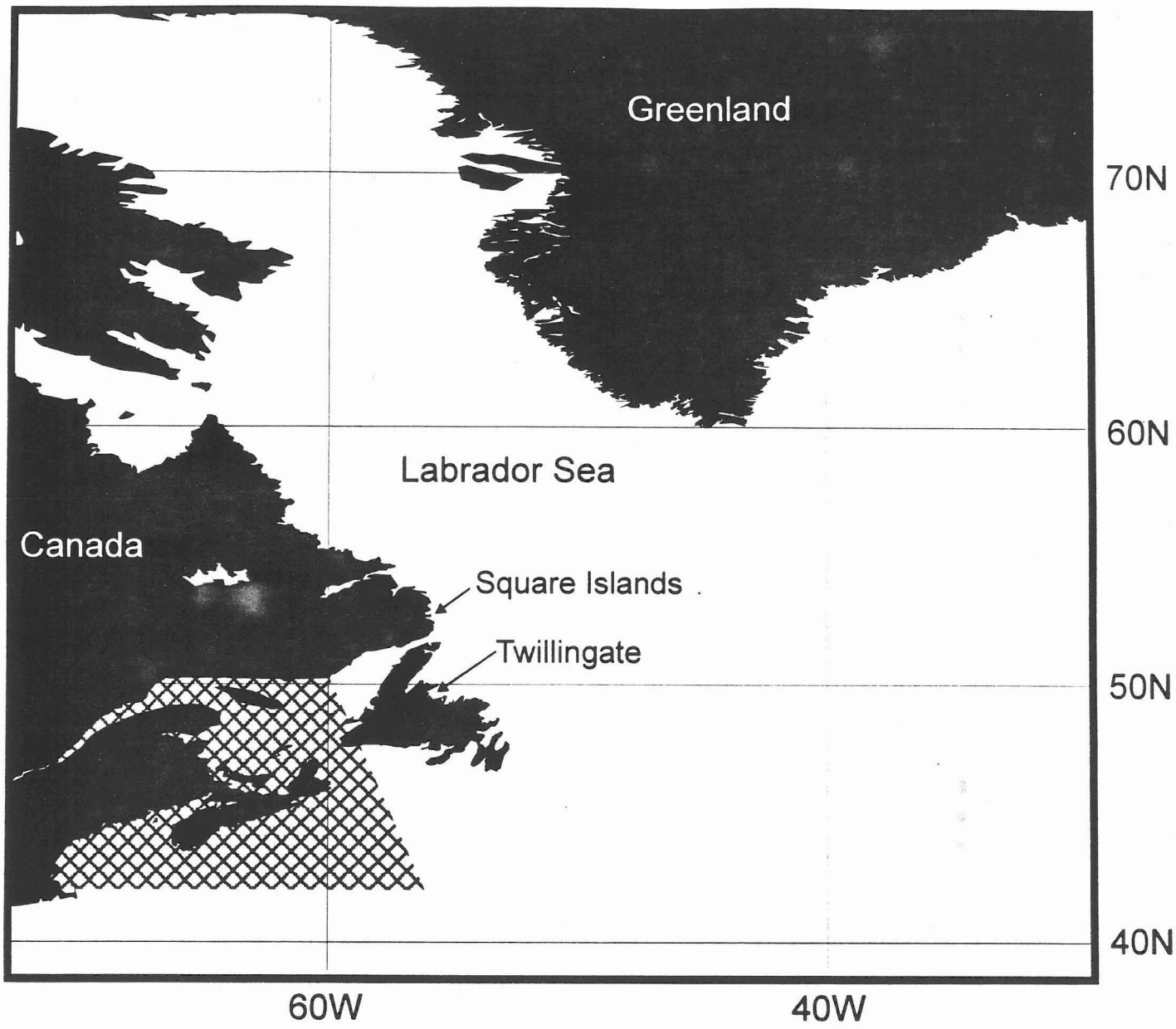
Sample	Country	Stock	Hatchery or Wild	Sea Age	River Age	Smolt Year	Date of Recapture	Date Sacificed	Length FL, cm
Immature Salmon									
A1	Ireland	Ballyshannon	H	1	1	1986	Sep-87	Sep-87	67
A3	UK	R. Wear	W	1	3	1986	Oct-87	Oct-87	69
A4	UK	R. Thames	H	1	-	1986	Sep-87	Sep-87	65
A5	Ireland	Inniscarra	H	1	-	1986	Sep-87	Sep-87	74
G1	Ireland	Inniscarra	H	1	1	1986	Sep-87	Sep-87	66
G2	Scotland	R. Lussa	H	1	-	1986	Oct-87	Oct-87	69
G3	Ireland	Galway	H	1	1	1986	Oct-87	Oct-87	68
G4	UK	R. Tees	H	1	1	1986	Sep-87	Sep-87	70
B1	USA	Penobscot	H	1	1	1986	Sep-87	Sep-87	61
B3	USA	Penobscot	H	1	1	1986	Sep-87	Sep-87	65
F1	Canada	Nepisiguit	H	1	2	1986	Sep-87	Sep-87	67
F2	Canada	Miramichi	H	1	-	1986	Sep-87	Sep-87	65
F3	USA	Penobscot	H	1	1	1986	Sep-87	Sep-87	61
F4	Canada	Nepisiguit	H	1	1	1986	Aug-87	Aug-87	64
P1	USA	Penobscot	H	1	1	1986	Aug-87	Aug-87	62
P2	USA	Penobscot	H	1	1	1986	Aug-87	Aug-87	61
P3	USA	Penobscot	H	1	1	1986	Aug-87	Aug-87	63
P4	USA	Penobscot	H	1	1	1986	Aug-87	Aug-87	63
P5	USA	Penobscot	H	1	-	1986	Aug-87	Aug-87	59
D2	Unknown	Unknown	W	1	3	1987	Sep-88	Sep-88	68
D3	Unknown	Unknown	W	1	3	1987	Aug-88	Aug-88	65
D4	Unknown	Unknown	W	1	5	1987	Sep-88	Sep-88	60
D5	Unknown	Unknown	W	1	3	1987	Sep-88	Sep-88	68
E1	Unknown	Unknown	W	1	5	1987	Sep-88	Sep-88	64
E2	Unknown	Unknown	W	1	4	1987	Sep-88	Sep-88	68
E3	Unknown	Unknown	W	1	4	1987	Sep-88	Sep-88	65
E4	Unknown	Unknown	W	1	5	1987	Sep-88	Sep-88	63
E5	Unknown	Unknown	W	1	4	1987	Sep-88	Sep-88	61
Maturing Salmon									
C1	USA	Merrimack	W	2	2	1992	May-94	Dec-94	80
C3	USA	Merrimack	W	2	2	1992	Jun-94	Dec-94	75
H1	USA	Penobscot	H	1	1	1994	Jul-95	Jul-95	52
H2	USA	Penobscot	H	1	1	1994	Jul-95	Jul-95	57
H3	USA	Penobscot	H	1	1	1994	Jun-95	Jun-95	54
H4	USA	Penobscot	H	1	1	1994	Jun-95	Jun-95	52
H5	USA	Penobscot	H	1	1	1994	Jun-95	Jun-95	57
I1	USA	Penobscot	H	1	1	1994	Jun-95	Jun-95	51
I2	USA	Penobscot	H	1	1	1994	Jun-95	Jun-95	57
I3	USA	Penobscot	W	1	2	1994	Jun-95	Jun-95	58
I4	USA	Penobscot	H	1	1	1994	Jun-95	Jun-95	53
I5	USA	Penobscot	H	1	1	1994	Jun-95	Jun-95	54
I6	USA	Penobscot	H	1	1	1994	Jun-95	Jun-95	52

Table 3. Minimum and maximum Sr:Ca ratios from the freshwater portion of salmon otoliths, and maximum and outer edge Sr:Ca ratios from the marine portion of salmon otoliths.

	Freshwater Sr:Ca		Marine Sr:Ca		Max-Edge
Sample	min	max	max	edge	Difference
Immature Salmon					
A1	0.00102	0.00131	0.00254	0.00217	0.00037
A3	0.00137	0.00217	0.00246	0.00227	0.00019
A4	0.00008	0.00020	0.00031	0.00028	0.00003
A5	0.00051	0.00066	0.00208	0.00177	0.00032
G1			0.00281	0.00203	0.00077
G2	0.00076	0.00078	0.00202	0.00172	0.00029
G3	0.00040	0.00128	0.00241	0.00189	0.00052
G4	0.00051	0.00061	0.00217		
Mean	0.00067	0.00100	0.00210	0.00173	0.00036
B1	0.00096	0.00123	0.00222	0.00190	0.00032
B3	0.00112	0.00139	0.00240	0.00186	0.00054
F1	0.00050	0.00095	0.00211	0.00146	0.00065
F2	0.00044	0.00119	0.00187	0.00169	0.00018
F3	0.00094	0.00125	0.00211	0.00174	0.00037
F4			0.00218	0.00178	0.00040
P1			0.00237	0.00182	0.00055
P2			0.00199	0.00165	0.00034
P3			0.00237	0.00175	0.00062
P4			0.00215	0.00167	0.00048
P5			0.00217	0.00217	0.00000
Mean	0.00079	0.00120	0.00218	0.00177	0.00040
D2	0.00122	0.00158	0.00227	0.00227	0.00000
D3	0.00062	0.00067	0.00254	0.00210	0.00044
D4	0.00105	0.00166	0.00247	0.00229	0.00018
D5	0.00153	0.00181	0.00235	0.00201	0.00035
E1			0.00227	0.00203	0.00024
E2			0.00235	0.00214	0.00021
E3			0.00261	0.00170	0.00091
E4			0.00200	0.00200	0.00000
E5			0.00249	0.00246	0.00003
Mean	0.00110	0.00143	0.00237	0.00211	0.00026
Maturing Salmon					
C1	0.00127	0.00157	0.00240	0.00193	0.00047
C3	0.00113	0.00126	0.00210	0.00174	0.00036
Mean	0.00120	0.00142	0.00225	0.00183	0.00042
H1	0.00140	0.00149	0.00188	0.00155	0.00033
H2	0.00117	0.00158	0.00214	0.00204	0.00010
H3			0.00204	0.00190	0.00014
H4	0.00153	0.00188	0.00200	0.00200	0.00000
H5			0.00192	0.00185	0.00008
I1			0.00177	0.00171	0.00006
I2			0.00205	0.00205	0.00000
I3			0.00206	0.00171	0.00035
I4			0.00219	0.00215	0.00005
I5			0.00208	0.00185	0.00023
I6			0.00256	0.00187	0.00069
Mean	0.00137	0.00165	0.00206	0.00188	0.00018
Grand Mean	0.00093	0.00126	0.00218	0.00187	0.00030
Stand. Dev.	0.00041	0.00048	0.00038	0.00034	0.00023
CV, %	44	38	17	18	77

List of Figures

Figure 1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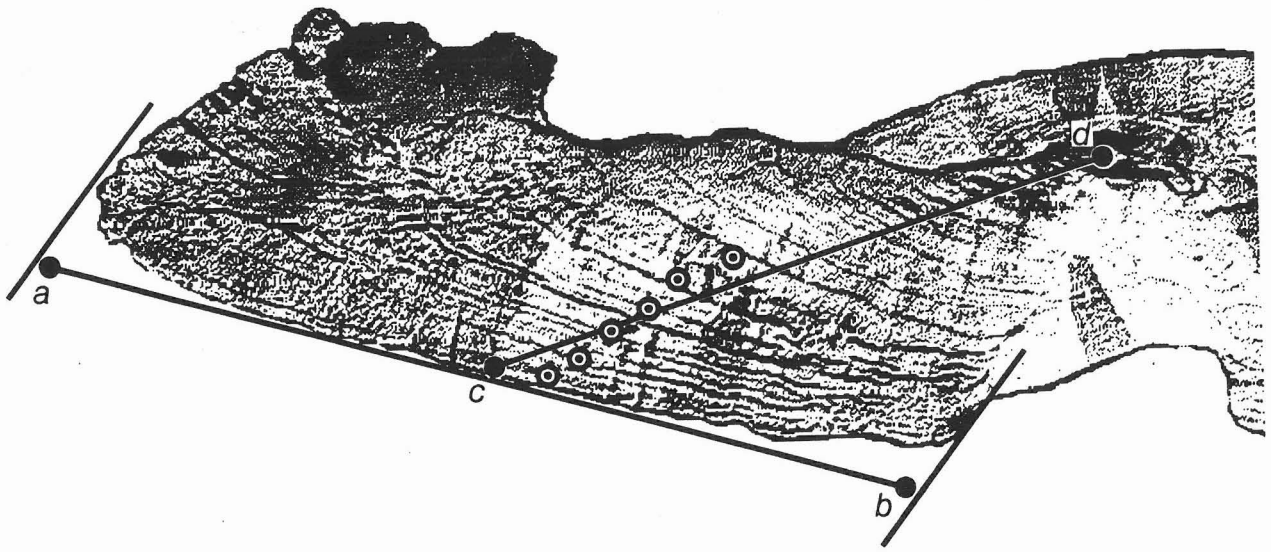
60N
Labrador Sea
Canada
Square Islands
Twillingate
50N
40N
60W
40W

Figure 2.

A



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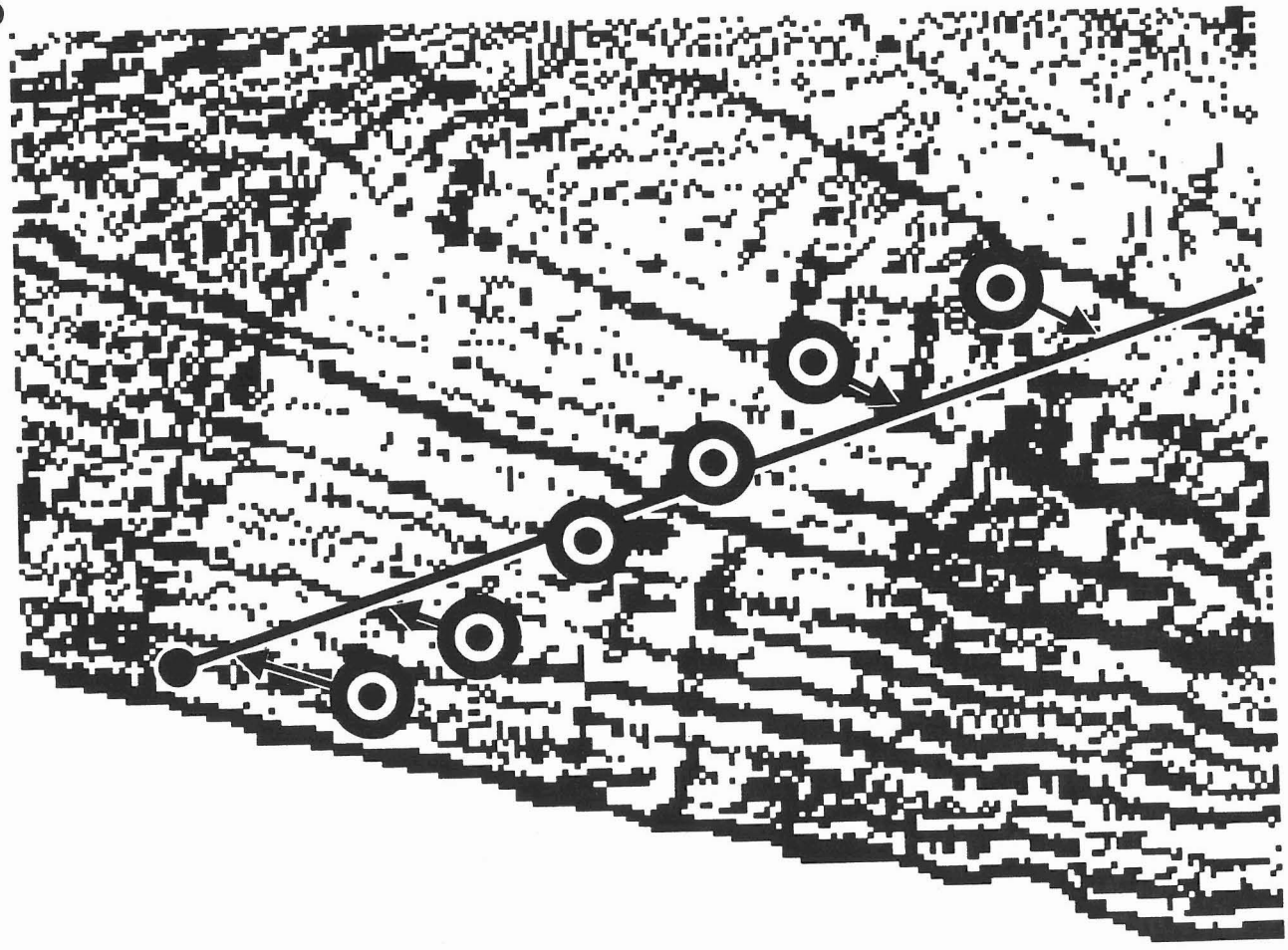

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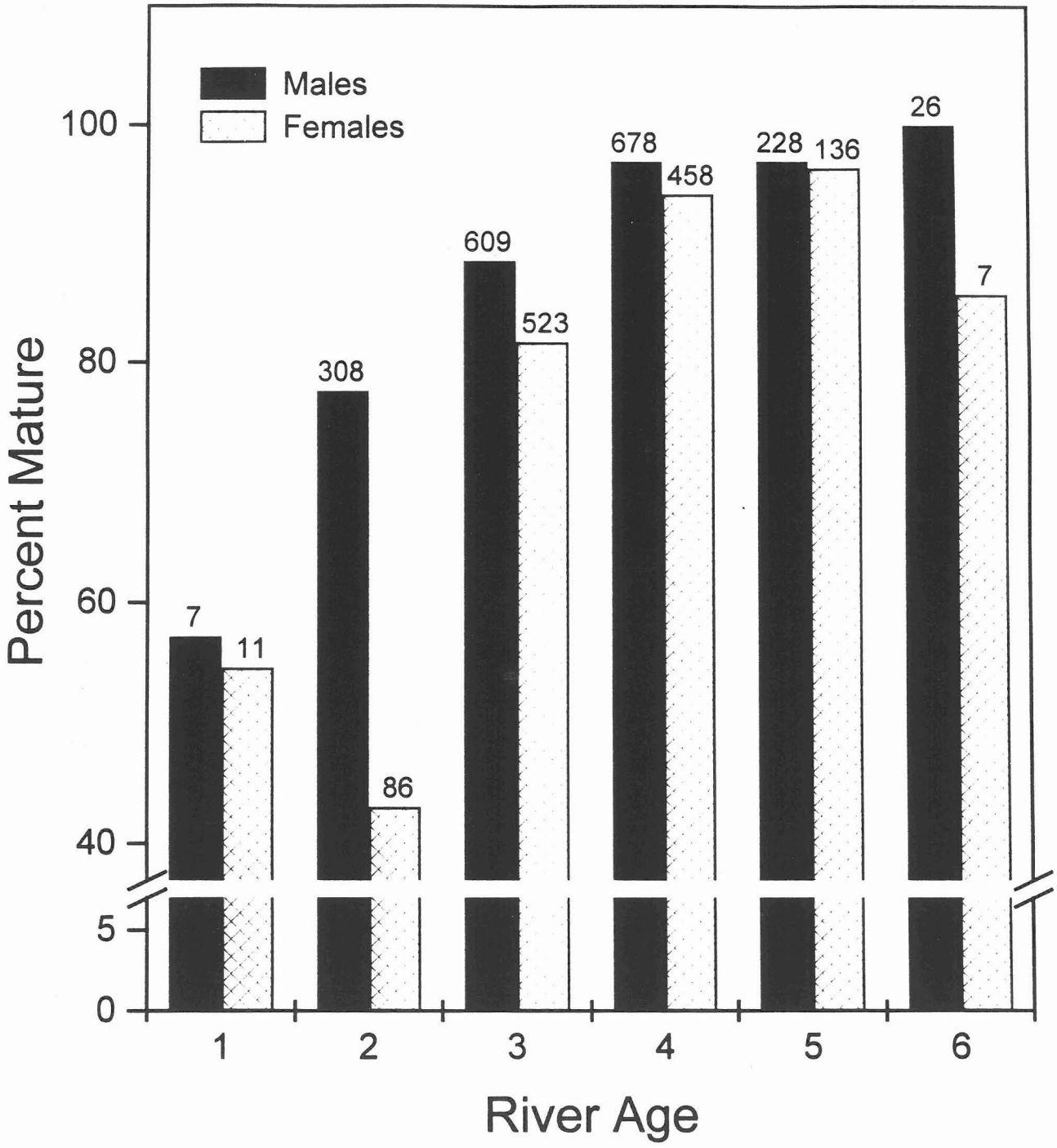
Males
Females
Percent Mature
100
80
60
40
5
0
7
11
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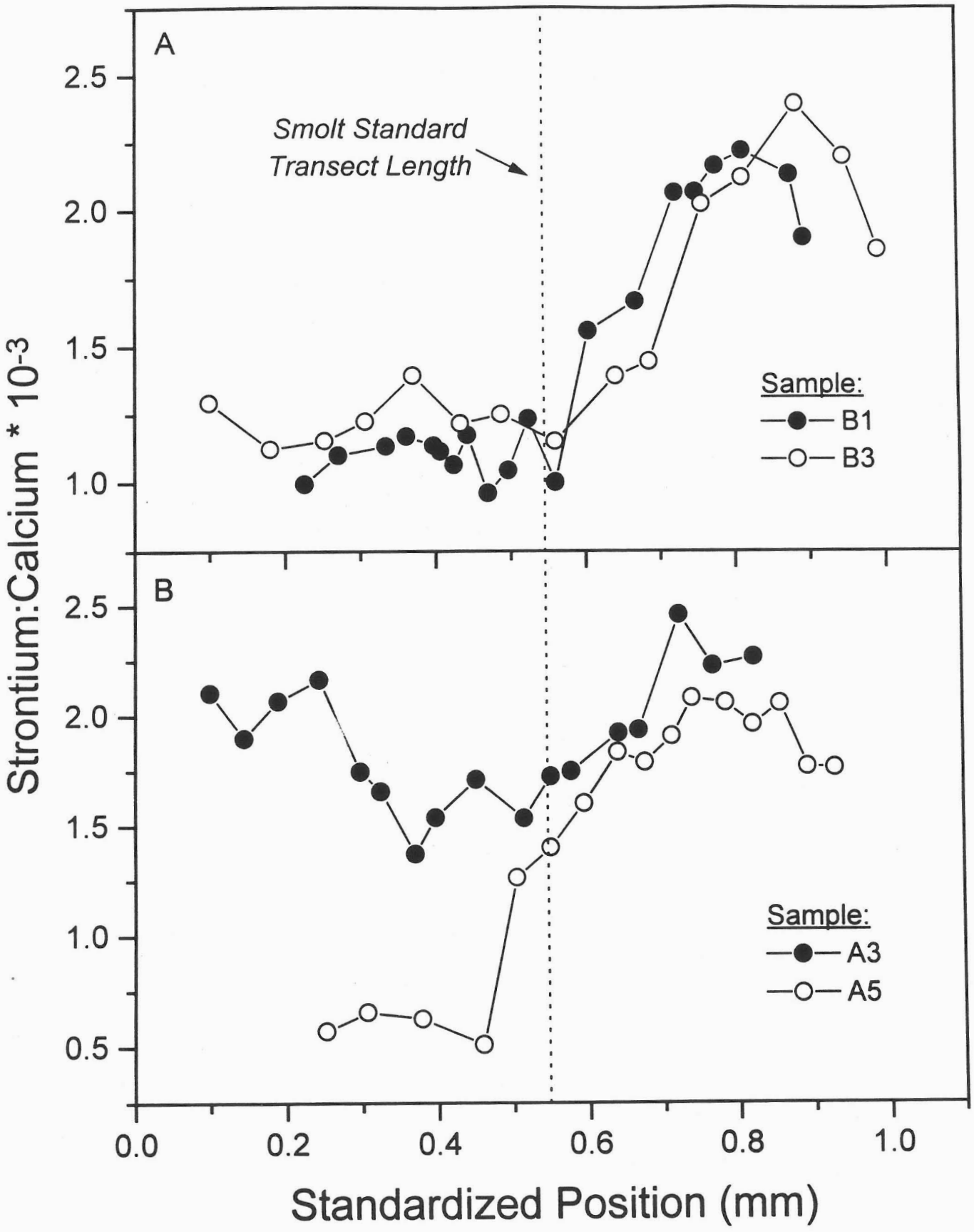
86
609
523
678
458
228
136
26
7
1
2
3
4
5
6
River Age

Figure 4.


A
B
Smolt Standard
Transect Length
Sample:
B1
B3
Sample:
A3
A5
Strontium:Calcium * 10-3
Standardized Position (mm)
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2.0
1.5
1.0
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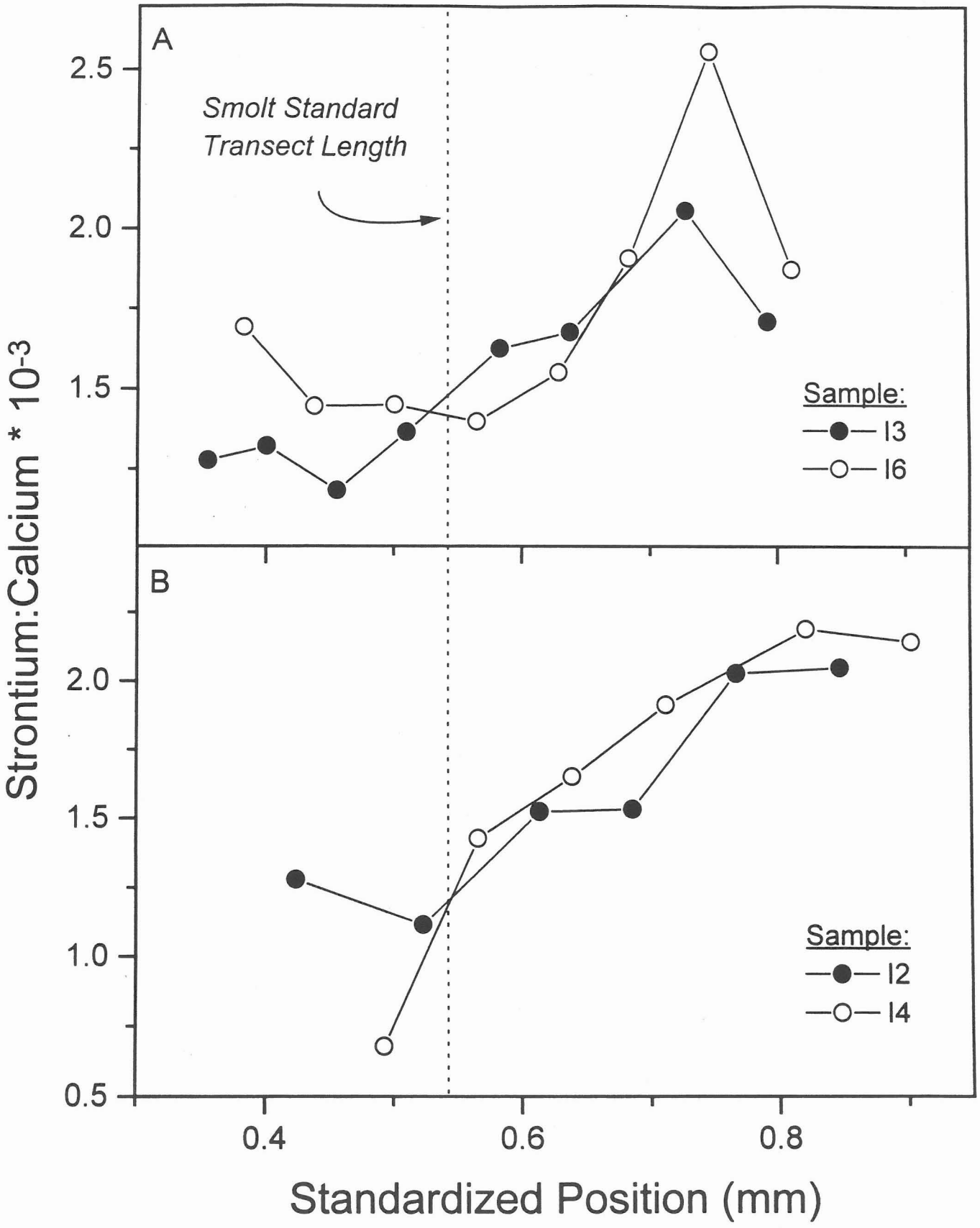
0.0
0.2
0.4
0.6
0.8
1.0

Figure 5.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I6
Sample:
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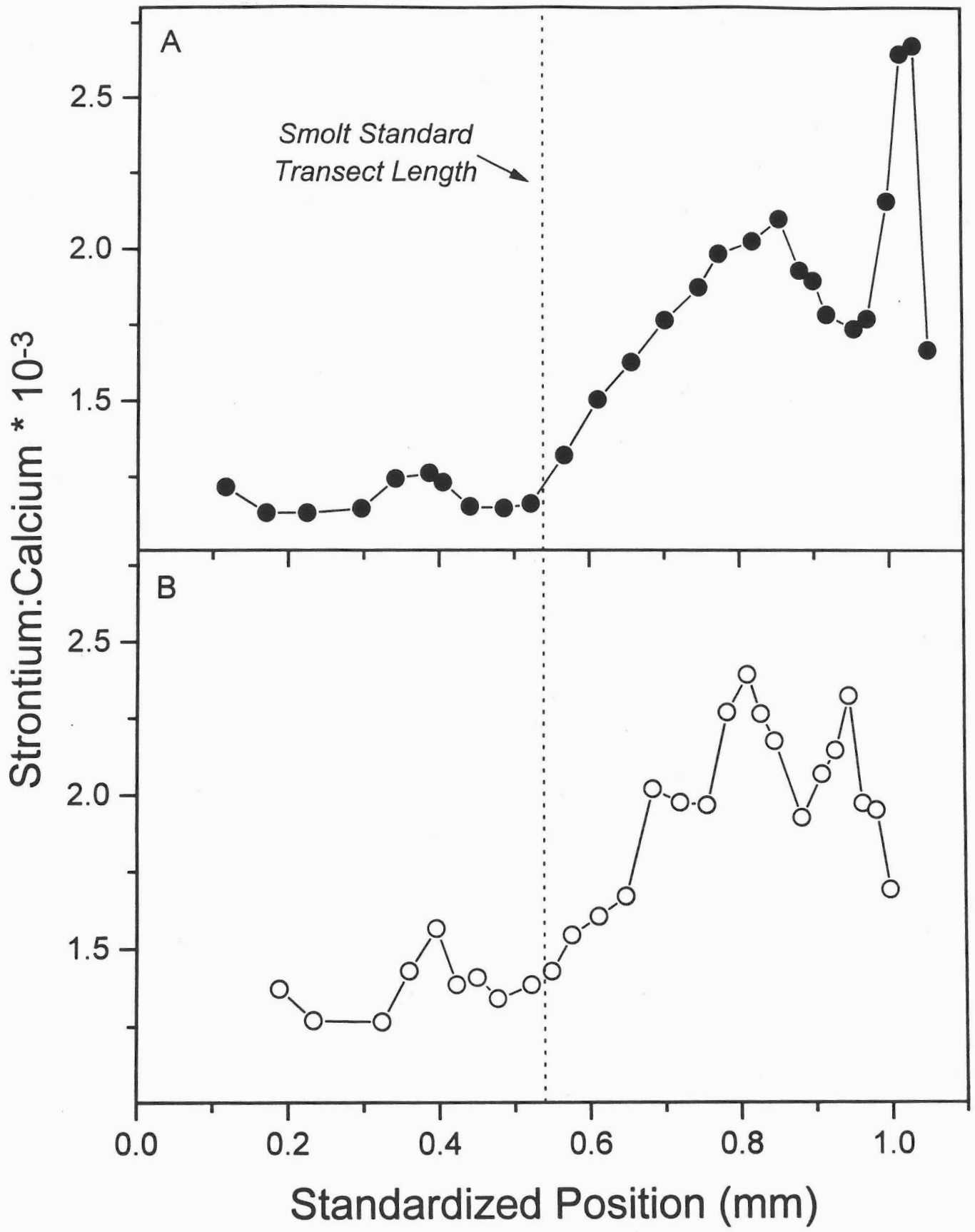
0.8
Strontium:Calcium * 10-3
Standardized Position (mm)

Figure 6.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B
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Transect Length
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1.5
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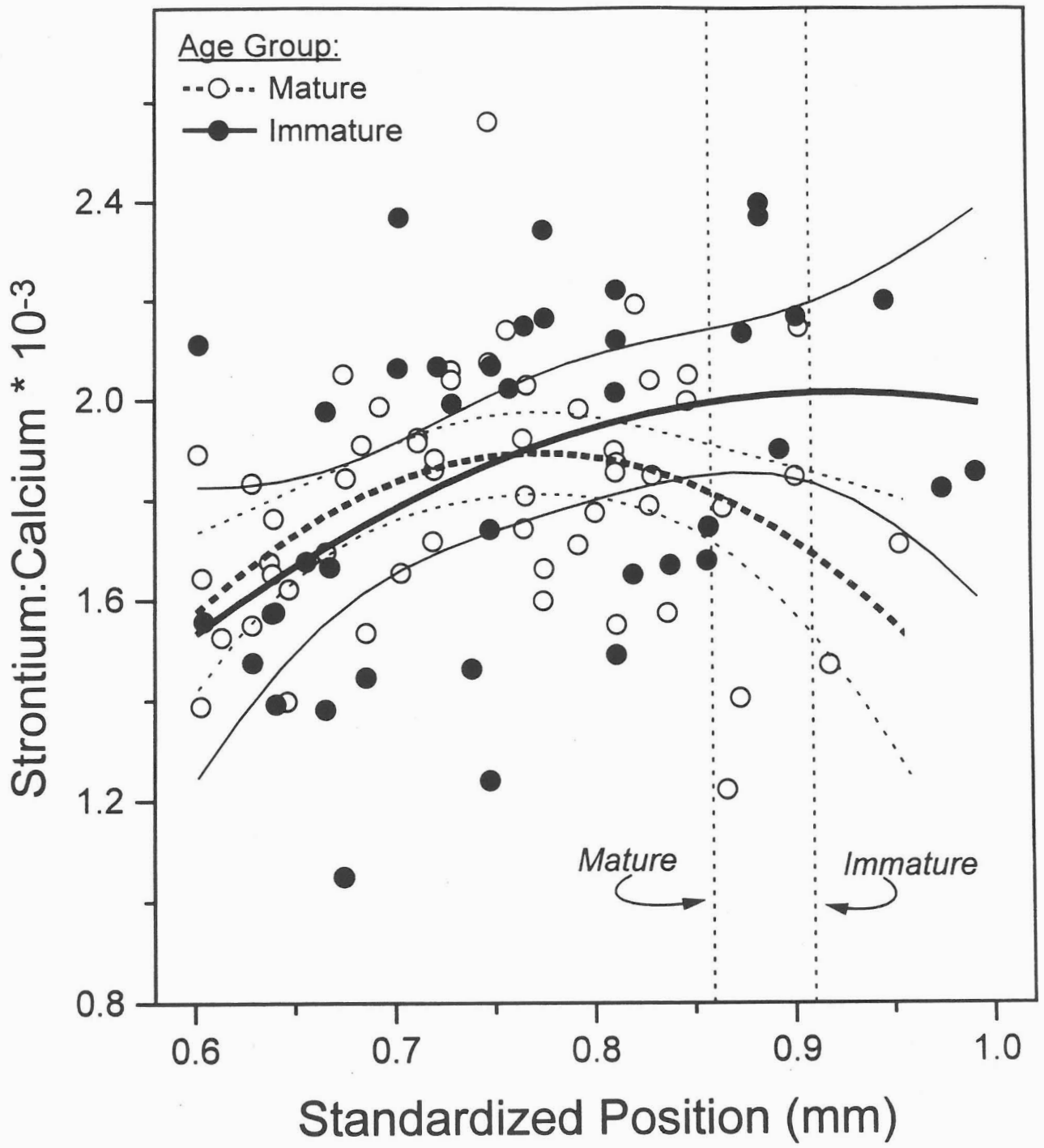
0.2
0.4
0.6
0.8
1.0
Standardized Position (mm)

Figure 7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Immature
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2.0
1.6
1.2
0.8
Strontium:Calcium * 10-3
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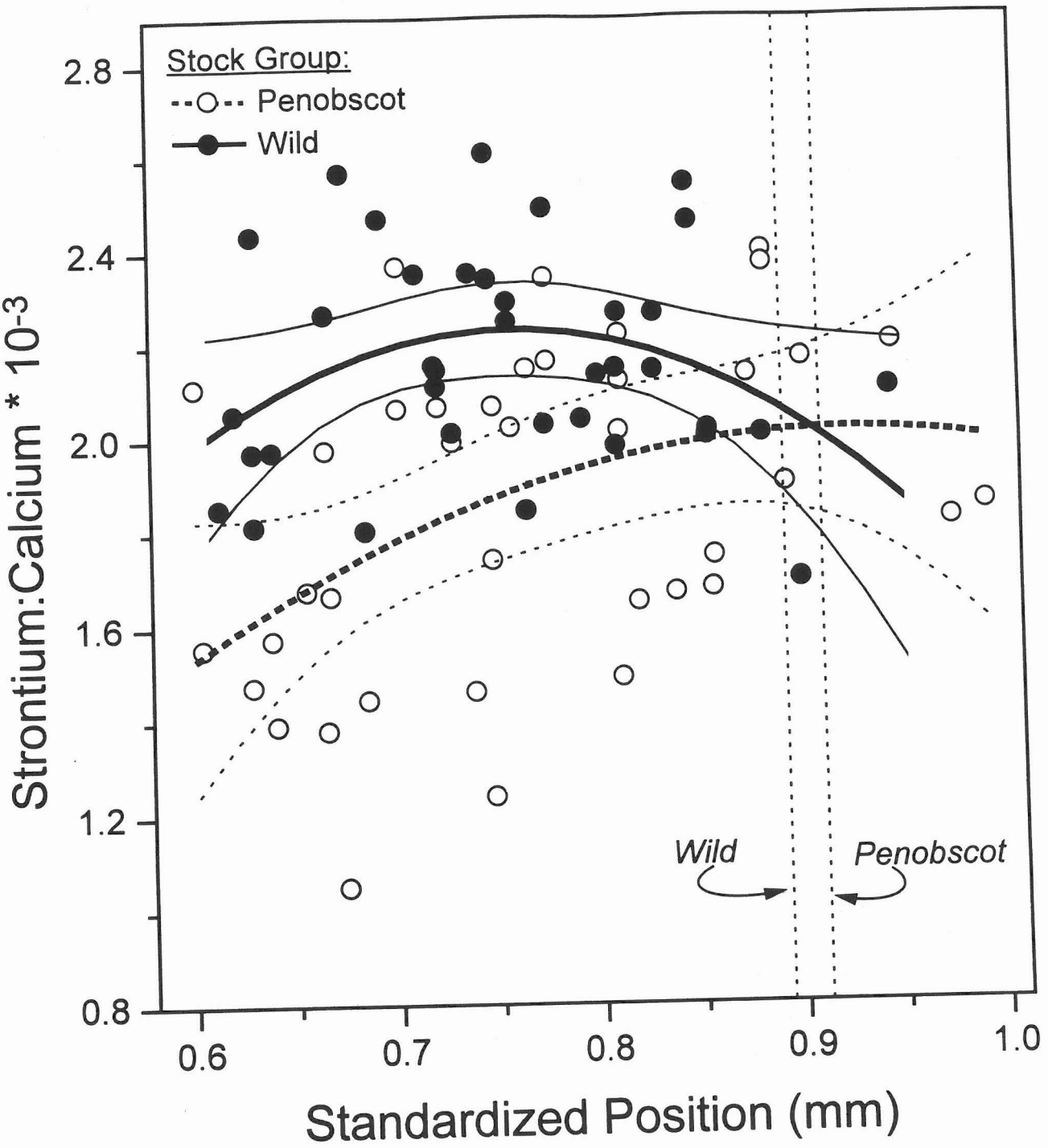
0.7
0.8
0.9
1.0
Standardized Position (mm)
Mature
Immature

Figure 8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1.6
1.2
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Strontium:Calcium * 10-3
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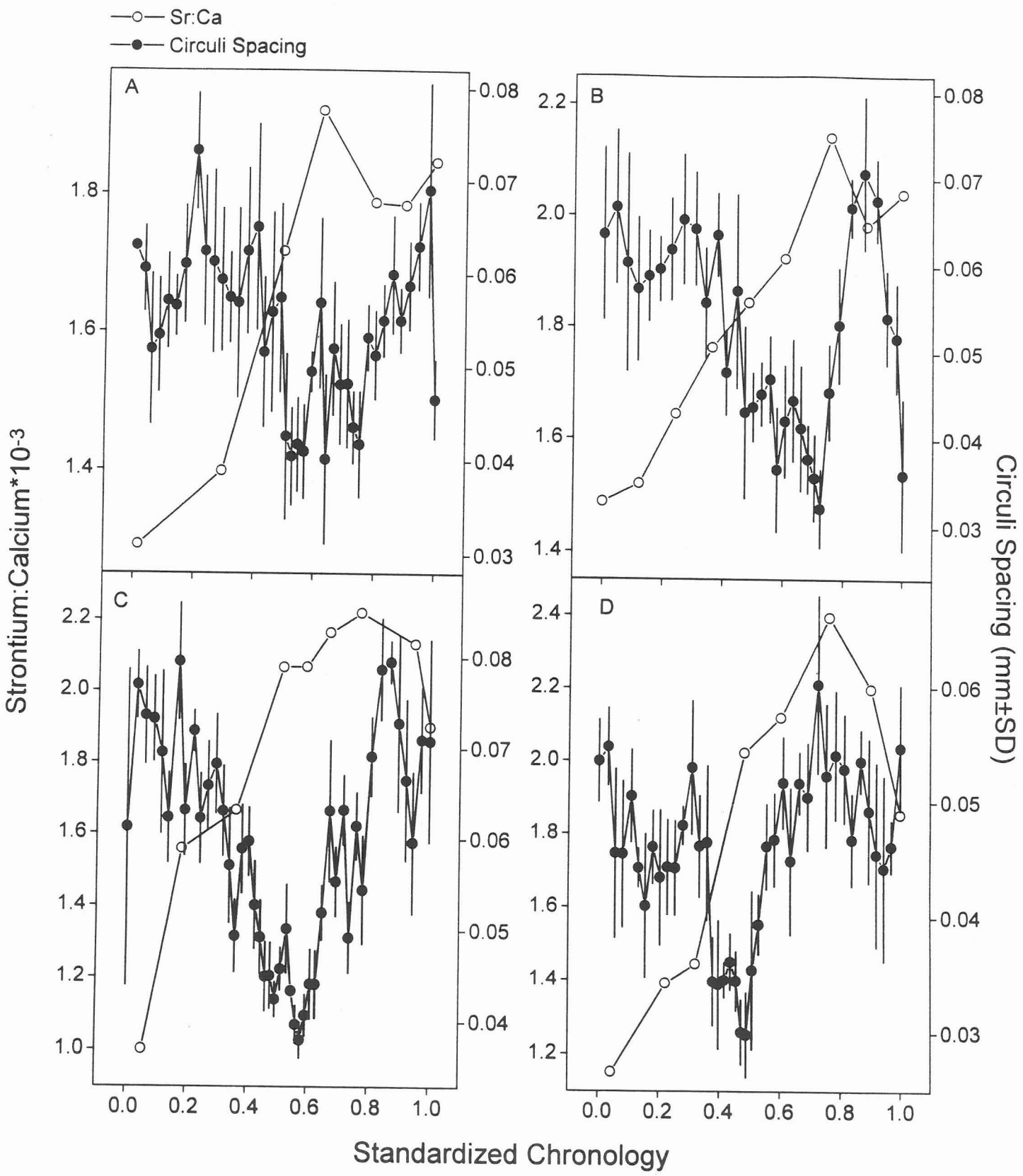
0.7
0.8
0.9
1.0
Standardized Position (mm)
Wild
Penobscot

Figure 9.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A
B
C
D
Strontium:Calcium*10-3
Circuli Spacing (mm±SD)
Standardized Chronology
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0.2
0.4
0.6
0.8
1.0