
Growth Patterns in Post-smolts Captured in the Labrador Sea and the Temporal Scale of Recruitment Coherence in North America

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Abstract.- We examined scale samples from historical collections of post-smolts made in the Labrador Sea with the aim of understanding the growth dynamics of stocks at the southern end of the range versus what is hypothesized to be the juvenile nursery for post-smolts from the entire stock complex. Circuli spacing patterns were extracted from the scales of 1,525 salmon collected from 1SW and 2SW returns to southern rivers and post-smolts collected in the Labrador Sea for three smolt years: 1988, 1989, and 1991. For two of the three years, growth trajectories for fish from the southern stocks intersected the trajectories for post-smolts from the Labrador Sea collections after 4-5 circuli pairs. Since circuli pairs are laid down at a rate of approximately one per fortnight, the data suggests that distribution patterns for regional groups begin to overlap and stocks begin to experience similar environmental conditions by July of the post-smolt year or two months after their migration to sea. In some years, it would appear regional groups do not mix until fall. These data provide the first indication of the mixing processes between stocks and may be useful in understanding regional patterns of recruitment coherence in salmon versus coherence patterns associated with the entire North American stock complex.

Key Words: Atlantic salmon, circuli spacing, migration, post-smolt growth, recruitment

Introduction

Recruitment coherence is being described on both regional and continental scales for Atlantic salmon. Regional coherence has been described with data for both wild and hatchery stocks (Friedland et al. 1993; Friedland et al. 1996; Friedland et al. 1998a). In these examples, tagged stocks show similar patterns of survival rate by cohort suggesting survival effects during the post-smolt year define recruitment to spawning. Continental and sub-continental coherence can be seen in long-term catch data for both North American and European stocks (Friedland et al. 1993). Furthermore, tele-connections between continental stock complexes are also evident in these catch time series (Friedland submitted). Recruitment patterns for Atlantic salmon appear to respond to ocean climate change in much the same way as continental stock complexes of Pacific salmon have responded to regime shifts in the North Pacific (Mantua et al. 1997). Perhaps with the most notable difference being regime shifts in the Pacific appear to reflect a more rapid change in climate state whereas change has been more gradual in the North Atlantic.

A consequence of coherence is the suggestion that synchronous stocks must either overlap in time and space or reside in large regions that are relatively uniform in their climate conditions and productivity. Which of these two possibilities exist for salmon is an important question, but equally important is at what time during the critical post-smolt year do conditions acting on a stock begin to

affect coherent stocks equivalently. Recruitment variability is attributed to mortality that occurs on stocks during their first year at sea; and, most of this mortality is believed to occur a short time after smolts enter the sea. This contention is supported by mortality rate estimates with tagging experiments in the Baltic region (Eriksson 1994) and indirectly by relationships between regional climate and survival (Friedland et al. 1998a). However, if survival is defined during this early segment of the post-smolt year, it occurs when stocks do not necessarily overlap on a continental scale. Thus, synchrony in recruitment is more likely to occur on a regional scale or reflect some other effect, such as maturation, which may act on stocks later in the post-smolt year and over larger spatial scales (Friedland et al. 1998b).

In this study we applied scale analysis to attempt to differentiate the temporal scales of regional versus continental coherence. We examined scale growth signatures from a mixed stock group of post-smolt salmon captured in the Labrador Sea to the signatures for a group of hatchery stocks from the southern range of salmon in North America.

Materials and Methods

We collected scale circuli spacing patterns representative of post-smolt growth for juvenile salmon captured in the Labrador Sea and for three index stocks from the southern portion of the range of salmon in North America. Labrador Sea post-smolt salmon were collected in 1988, 1989, and 1991 in a directed research survey (Reddin and Short 1991). These post-smolts were captured in gill nets over a series of stations in the Labrador Sea during the fall of the year, mostly in the month of October (Fig. 1). Data for comparative purposes come from the returning adults of hatchery origin fish from the Connecticut, Penobscot, and Saint John rivers, all located south of the Gulf of St. Lawrence (Fig. 1). The data for the Connecticut and Penobscot have been presented earlier (Friedland et al. 1996); whereas, the Saint John data is newly reported here. Sample sizes sorted by smolt year of migration to sea and age of maturity are reported in Table 1. The low number of 1SW returns to the Connecticut River did not provide sufficient samples for their inclusion in this study.

Post-smolt growth was interpreted from circuli spacing patterns deposited during the post-smolt year. Scales were cleaned and mounted between glass slides and the spacing of scale circuli were measured with a Bioscan Optimas image processing system (reference to tradename does not suggest endorsement). The first spacing was measured between the first circulus of the post-smolt growth zone and the next circulus, and continued with successive pairs. For fish captured as post-smolts, measurements were taken to the edge of the scale (Fig. 2A). For maturing fish returning to their natal river after at least year one winter at sea, the measurements were made through the first seawinter annulus of the scale and thus captured the entire post-smolt growth zone (Fig. 2B). We only needed to use a subset of the data collected from maturing fish in order to match the spacing data collected from the post-smolt samples. Measurements were made on a single scale from each specimen at a pixel resolution of 0.004 mm along the 360° axis of the scale. Additionally, the river age distributions for Labrador Sea post-smolt specimens were determined with conventional aging.

Return rates by sea-age and fraction of the smolt cohort maturing after one-seawinter (1SW) were computed for the three stocks used for comparison. Return rates are simple percentages of the number of returns-at-age to the number of smolts released either one or two year prior. Return rates for the Connecticut and Penobscot stocks originally reported in (Friedland et al. 1996) are updated here. Return rates for the Saint John stock were computed similarly and are based on smolt releases of 142, 238, and 178 thousand smolts for the years 1988, 1989, and 1991. Releases over the period 1974-1992 averaged approximately 200 thousand smolts in the St. John system. The fraction of the smolt cohort maturing after one-seawinter, the 1SW Fraction, was computed using the formulae of Friedland et al. (1996). Likewise, these data are updated for the Connecticut and Penobscot stocks and newly reported

for the Saint John.

Circuli spacing data for Gulf of St. Lawrence post-smolts were compared in two ways. First, data for the Labrador Sea post-smolt scales were compared over the years 1988, 1989, and 1991. The spacings for the first fifteen circuli pairs were compared with ANOVA. This and subsequent statistical analyses were restricted to the first fifteen circuli pairs because the number of circuli deposited is a function of age and sampling date, thus most scales did not have data for the higher number circuli pairs. Therefore, spacing patterns for circuli pairs beyond pair number 15 are not well estimated. For the second comparison, post-smolt scale samples were compared to the data for the three comparison stocks. The data for the comparison stocks were separated by their smolt year; thus, the post-smolt scale data were compared to the available return age components for a given smolt year and stock. The statistical comparison was simplified to a two group ANOVA, comparing circuli spacing of the first fifteen circuli pairs of the post-smolts to each smolt year, age combination.

Results

Circuli spacing patterns for the post-smolt growth zones of Labrador post-smolts were similar for the three year classes we examined. These fish ranged in river ages of 1 to 7 years, with over 80% of the fish falling into ages 2-4 years (Table 2). The mode age was either 2 or 3 years. Circuli spacing for the first few pairs, associated with the first few weeks in the marine environment, were similar in all three years, measuring approximately 0.029 to 0.048 mm (Figure 3). Beyond these initial pairs, the spacings were nearly the same except for some minor differences around circuli pair nine. Spacings during the summer growth period ranged from approximately 0.055 to 0.077 mm. ANOVA results suggest that the yearly spacing means are not significantly different for any of the first fifteen spacing pairs (Table 3).

Circuli spacing patterns for Labrador Sea post-smolts were markedly different from the patterns observed for other stocks. Relevant to all stock comparisons, we found that the post-smolt specimens had narrower circuli spacings during the early period at sea compared to spacings for the specimens from the southern stocks. However, spacing patterns for the balance of the period and limited to first fifteen circuli pairs spacings were similar. For Connecticut River 2SW returns, post-smolt growth trajectories do not intersect post-smolt trajectories for the Labrador Sea post-smolts until after 5 to 7 circuli pairs (Figure 4). ANOVA suggest that there are significant differences between these pairs and also somewhat of an inconsistent pattern of differences between the stocks at the higher circuli pairs (Table 4). In particular, Connecticut River spacing patterns appear to be less than the post-smolts in the years 1988 and 1991 (Figs. 4A and 4C). Penobscot spacing patterns also show larger spacing in the beginning of the post-smolt year; however, and with few exceptions, higher circuli pairs do not diverge from the spacings observed for the post-smolts (Fig. 5). The statistical comparison shows that for 1988 and 1989, 1SW and 2SW Penobscot spacings are different for either the first 4 or 5 spacings only (Table 4). In 1991, the differences exist for the first 10 and 8 pairs for 1SW and 2SW fish, respectively. Only pairs 13-15 for Penobscot 2SW fish are significantly narrower than post-smolt spacings. In the Saint John, we observed some systematic differences between 1SW and 2SW salmon patterns, but overall growth patterns related to the post-smolts patterns in much the way as the Penobscot data (Fig. 6). One of the more interesting contrasts was the number of early season circuli pairs at variance to the post-smolt data. For the Saint John 2SW returns, the spacings for the first 3 and 4 pairs were significantly different from post-smolt spacings during 1988 and 1989, respectively (Table 4). In 1991, growth patterns for the Saint John do not intersect the post-smolt data until about the twelfth pair for both 1SW and 2SW salmon.

The three stocks provided for comparison to Labrador post-smolts display a range of return rates and 1SW fraction reflecting differences in survival and maturity rates. For the Connecticut stock, return

rate of 2SW fish and 1SW fraction averaged 0.13% and 0.01, respectively (Table 5). Penobscot River smolts returned at higher rates, 0.09% and 0.47% for 1SW and 2SW fish, respectively. Typically 10% of the Penobscot cohort matures at 1SW. The Saint John stock had the highest return rates and largest proportion of the cohort maturing after one-seawinter. The return rate for 1SW fish averaged 1.47% and the 1SW Fraction averaged 0.59. The 2SW return rate for the Saint John is similar to that observed for the Penobscot stock. Thus, the Connecticut stock had the lowest survival and produced few early maturing fish, the Saint John had the highest survival and produced many early maturing fish, and the Penobscot stock was intermediate between the other two.

Discussion

Our principal finding was the suggestion from the circuli spacing data that continental stock mixing occurs after a period of time related to the deposition of four to eight circuli pairs. The samples of post-smolts from the Labrador Sea had an age composition typical of a cross-section of North American salmon stocks (Power 1981; Saunders 1981). Additionally, this mixed stock group of fish was destined to spawn the year following capture as 2SW salmon because of the time and location of capture. The 2SW returns to the Penobscot and Saint John stocks intersect and generally overlap the composite trajectory for the mixed stock group after approximately four circuli pair. The more southerly stock, the 2SW Connecticut fish, appear to have a greater delay before mixing with other stocks as suggested by the higher number of circuli pairs deposited before growth trajectories overlap.

The period of time it takes to deposit a circulus changes with season. Recaptures of post-smolts used in this study were analyzed to estimate the average date of deposition for specific circuli (Friedland et al. 1993). These data suggested that circuli deposition is spaced by nearly a week during the spring and summer growth seasons and progressively slows to nearly two weeks by winter. This would suggest Penobscot and Saint John fish do not overlap the bulk of other North America stocks for as little as one month after migration to the sea in some years. However, this period of regional isolation may last for periods longer than one month.

The higher growth of southern stocks during the critical early period of marine residency may confer a survival advantage to southern fish. Size mediated predation interactions are likely a critical factor for Atlantic salmon post-smolts during the first months at sea (Holtby et al. 1990; L'Abée-Lund et al. 1993). Though these fish may be growing faster than their counterparts from more northern stocks, they are also potentially overlapping a more diverse predator field of other species entering the Gulf of Maine and the Scotian Shelf during the spring period.

These data allow us to suggest a frame of reference for the temporal scale of regional versus continental coherence of North America salmon stocks. Regional effects would be expected to dominate an individual salmon stock for at least the first month at sea. The temporal scale of regional coherence also implies limits for the spatial scale of regional coherence. Since post-smolt salmon are in part passively transported during their first months at sea (Jonsson et al. 1993), using a combination of swimming potential and current transport vectors will circumscribe an area relevant to a specific stock. After a few months at sea, post-smolts attain sufficient size to begin to out-swim currents and will distribute according to thermal and feeding preferences. These factors should be taken into account when considering models and analyses that attempt to explain survival mechanisms mediated by climate factors. The spatial scale of any survival forcing function should be designed to match the likely spatial scale of the stock group being analyzed.

Acknowledgments

We thank L. Marshall, Department of Fisheries and Oceans, Halifax for providing scale material from the Mactaquac Hatchery and summary return rate data.

Table 1. Sample sizes for circuli spacing analysis by stock group and age of capture.

Stock	Age	Smolt Year		
		1988	1989	1991
Connecticut	2SW	170	121	178
Penobscot	1SW	70	105	89
	2SW	64	83	79
Saint John	1SW	73	95	90
	2SW	52	78	78
Labrador Sea	Post-Smolt	32	35	33

Table 2. River age distribution of post-smolts collected in the Labrador Sea.

Smolt Year	River Age										Total Number
	1		2		3		4		5+		
	Number	%	Number	%	Number	%	Number	%	Number	%	
1988	11	6.0	36	19.8	83	45.6	40	22.0	12	6.6	182
1989	18	8.7	72	34.6	69	33.2	30	14.4	19	9.1	208
1991	8	9.0	37	41.6	26	29.2	15	16.9	3	3.4	89

Table 3. Results of ANOVAs comparing the year effect in scale circuli spacing data from post-smolt specimens collected in the Labrador Sea, for smolt years 1988, 1989, and 1991.

Circuli			
Pair	DF	p-level	
1	2	.97	0.22
2	2	.97	0.97
3	2	.97	0.95
4	2	.97	0.80
5	2	.97	0.88
6	2	.97	0.86
7	2	.97	0.62
8	2	.97	0.48
9	2	.97	0.13
10	2	.97	0.86
11	2	.96	0.76
12	2	.95	0.27
13	2	.93	0.67
14	2	.91	0.31
15	2	.87	0.38

Table 4. Results of ANOVAs comparing the stock effect in scale circuli spacing data between post-smolt specimens collected in the Labrador Sea and three monitored stocks, for smolt years 1988, 1989, and 1991.

Stock	Circuli Pair	One Sea-winter Smolt Year						Two Sea-winter Smolt Year					
		1988		1989		1991		1988		1989		1991	
		DF	p-level	DF	p-level	DF	p-level	DF	p-level	DF	p-level	DF	p-level
Connecticut River	1							1,200	0.00 *	1,154	0.00 *	1,209	0.00 *
	2							1,200	0.00 *	1,154	0.00 *	1,209	0.00 *
	3							1,200	0.00 *	1,154	0.00 *	1,209	0.00 *
	4							1,200	0.00 *	1,154	0.00 *	1,209	0.00 *
	5							1,200	0.00 *	1,154	0.01 *	1,209	0.01 *
	6							1,200	0.56	1,154	0.01 *	1,209	0.00 *
	7							1,200	0.52	1,154	0.02 *	1,209	0.16
	8							1,200	0.11	1,154	0.29	1,209	0.23
	9							1,200	0.01 *	1,154	0.11	1,209	0.87
	10							1,200	0.54	1,154	0.60	1,209	0.01 *
	11							1,200	0.03 *	1,154	0.70	1,208	0.00 *
	12							1,200	0.84	1,153	0.14	1,208	0.00 *
	13							1,200	0.14	1,151	0.17	1,208	0.00 *
	14							1,198	0.00 *	1,151	0.03 *	1,208	0.00 *
	15							1,198	0.07	1,148	0.00 *	1,207	0.00 *
Penobscot River	1	1,100	0.00 *	1,138	0.00 *	1,120	0.00 *	1,94	0.00 *	1,116	0.00 *	1,110	0.00 *
	2	1,100	0.00 *	1,138	0.00 *	1,120	0.00 *	1,94	0.00 *	1,116	0.00 *	1,110	0.00 *
	3	1,100	0.00 *	1,138	0.00 *	1,120	0.00 *	1,94	0.00 *	1,116	0.00 *	1,110	0.00 *
	4	1,100	0.00 *	1,138	0.00 *	1,120	0.00 *	1,94	0.00 *	1,116	0.01 *	1,110	0.00 *
	5	1,100	0.00 *	1,138	0.24	1,120	0.00 *	1,94	0.08	1,116	0.23	1,110	0.00 *
	6	1,100	0.11	1,138	0.94	1,120	0.00 *	1,94	0.94	1,116	0.08	1,110	0.00 *
	7	1,100	0.74	1,138	0.35	1,120	0.00 *	1,94	0.80	1,116	0.06	1,110	0.00 *
	8	1,100	0.92	1,138	0.31	1,120	0.00 *	1,94	0.89	1,116	0.19	1,110	0.00 *
	9	1,100	0.36	1,138	0.85	1,120	0.00 *	1,94	0.30	1,116	0.61	1,110	0.27
	10	1,100	0.10	1,138	0.56	1,120	0.04 *	1,94	0.79	1,116	0.83	1,110	0.84
	11	1,100	0.92	1,138	0.70	1,119	0.23	1,94	0.76	1,116	0.70	1,109	0.44
	12	1,100	0.11	1,137	0.91	1,119	0.36	1,94	0.06	1,115	0.06	1,109	0.07
	13	1,100	0.18	1,135	0.86	1,119	0.88	1,94	0.62	1,113	0.59	1,109	0.05 *
	14	1,98	0.08	1,135	0.95	1,119	0.96	1,92	0.87	1,113	0.40	1,109	0.01 *
	15	1,98	0.65	1,132	0.50	1,118	0.35	1,92	0.11	1,110	0.34	1,108	0.00 *
Saint John	1	1,103	0.00 *	1,128	0.00 *	1,121	0.00 *	1,82	0.00 *	1,111	0.00 *	1,109	0.00 *
	2	1,103	0.00 *	1,128	0.00 *	1,121	0.00 *	1,82	0.00 *	1,111	0.00 *	1,109	0.00 *
	3	1,103	0.00 *	1,128	0.00 *	1,121	0.00 *	1,82	0.00 *	1,111	0.00 *	1,109	0.00 *
	4	1,103	0.00 *	1,128	0.00 *	1,121	0.00 *	1,82	0.13	1,111	0.00 *	1,109	0.00 *
	5	1,103	0.04 *	1,128	0.01 *	1,121	0.00 *	1,82	0.51	1,111	0.49	1,109	0.00 *
	6	1,103	0.42	1,128	0.04 *	1,121	0.00 *	1,82	0.16	1,111	0.84	1,109	0.00 *
	7	1,103	0.98	1,128	0.02 *	1,121	0.00 *	1,82	0.01 *	1,111	0.87	1,109	0.00 *
	8	1,103	0.54	1,128	0.17	1,121	0.00 *	1,82	0.18	1,111	0.63	1,109	0.00 *
	9	1,103	0.11	1,128	0.02 *	1,121	0.00 *	1,82	0.01 *	1,111	0.61	1,109	0.00 *
	10	1,103	0.49	1,128	0.09	1,121	0.00 *	1,82	0.03 *	1,111	0.37	1,109	0.02 *
	11	1,103	0.73	1,128	0.23	1,120	0.07	1,82	0.08	1,111	0.63	1,108	0.01 *
	12	1,103	0.03 *	1,127	0.78	1,120	0.04 *	1,82	0.42	1,110	0.18	1,108	0.02 *
	13	1,103	0.02 *	1,125	0.83	1,120	0.25	1,82	0.37	1,108	0.68	1,108	0.29
	14	1,101	0.96	1,125	0.78	1,120	0.65	1,80	0.01 *	1,108	0.67	1,108	0.06
	15	1,101	0.03 *	1,122	0.49	1,119	0.83	1,80	0.81	1,105	0.65	1,107	0.87

Table 5. Percent return rate by age group and 1SW fraction for three monitored stocks. Return rates are in percent where 1SW fraction is the proportion of a cohort maturing after one sea-winter. Mean is for the period smolt years 1974-1992.

Smolt Year	Connecticut		Penobscot			Saint John		
	2SW	Fraction	1SW	2SW	Fraction	1SW	2SW	Fraction
1988	0.06	0.00	0.13	0.37	0.17	0.81	0.36	0.58
1989	0.08	0.00	0.10	0.26	0.18	0.41	0.20	0.54
1991	0.04	0.01	0.14	0.19	0.32	0.74	0.13	0.79
Mean	0.13	0.01	0.09	0.47	0.12	1.47	0.57	0.59

List of Figures

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Figure 1

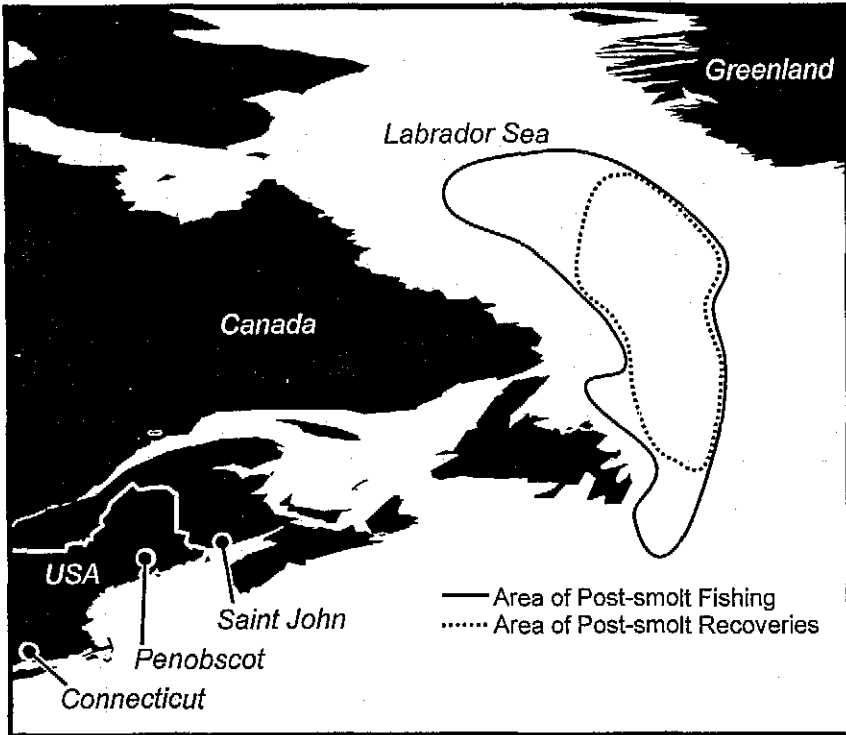


Figure 2

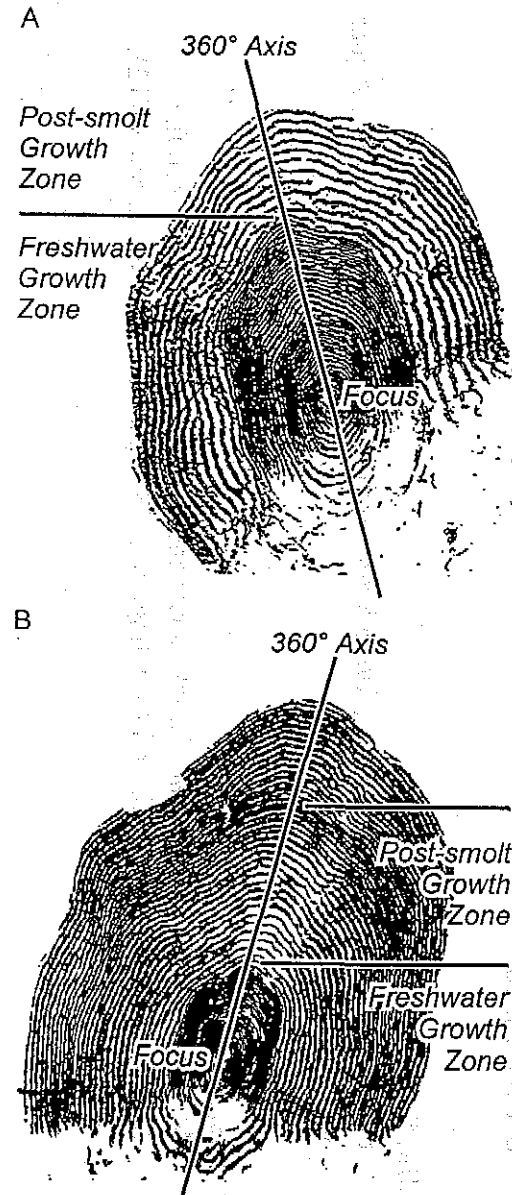


Figure 4

Figure 3

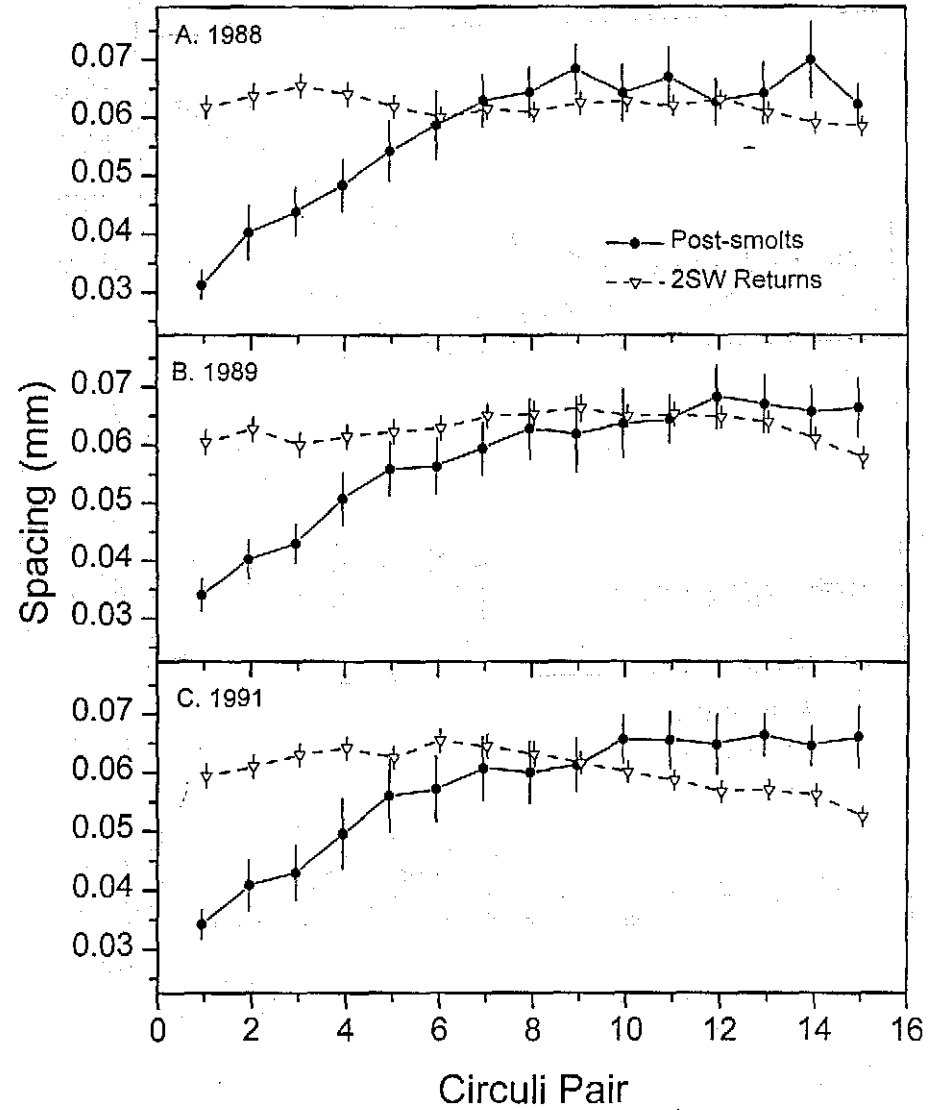
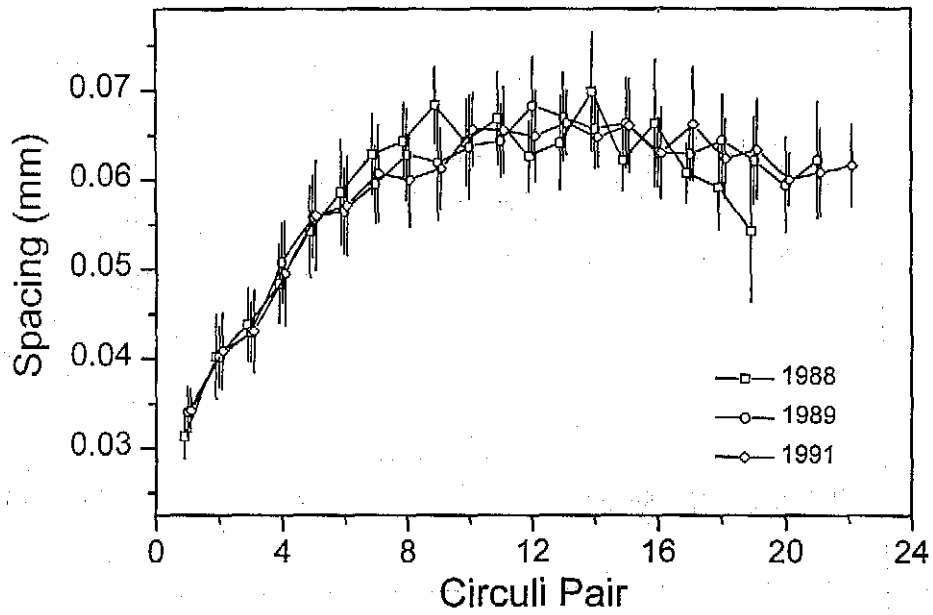


Figure 5

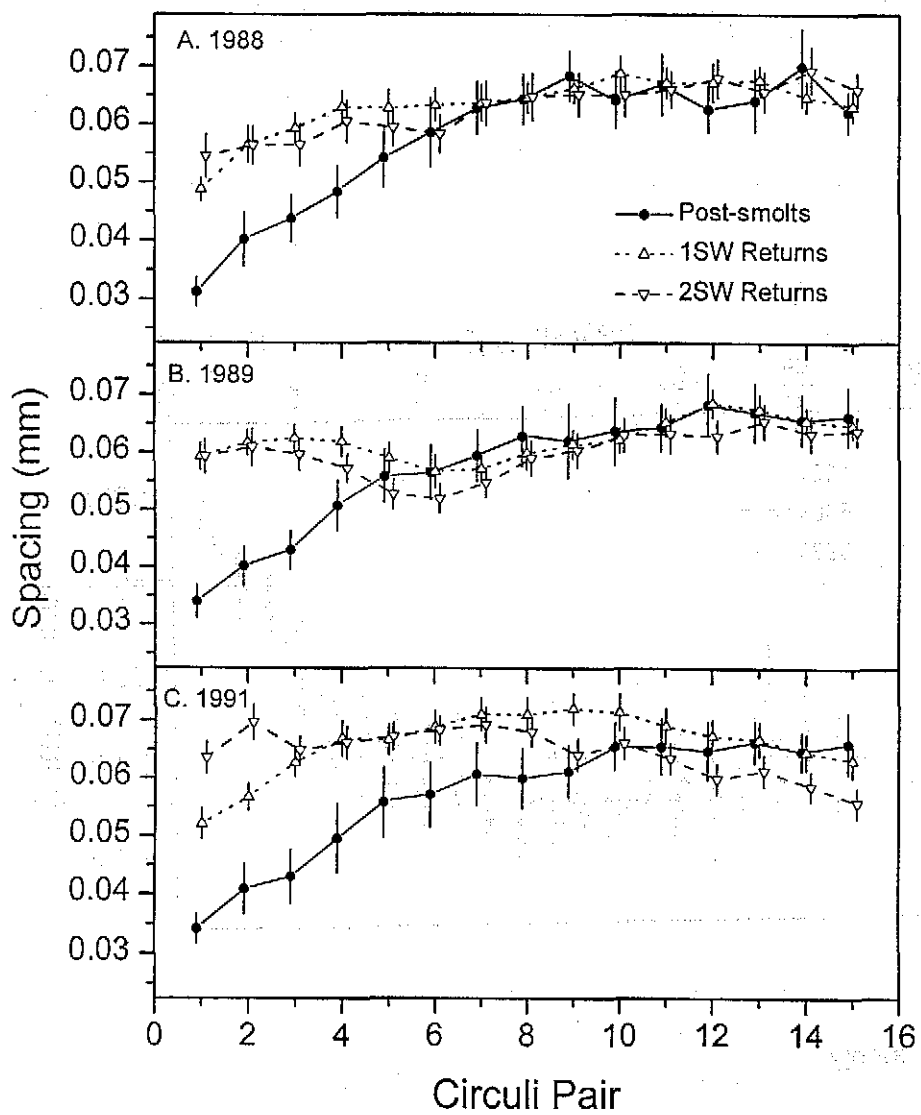


Figure 6

