Post-smolt Growth in Atlantic Salmon from North America and the Nature of Marine Juvenile Nurseries

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Abstract.- We examined scale samples from historical collections of post-smolts made in the Gulf of St. Lawrence, Canada, with the aim of understanding the role of estuarine and coastal habitats as juvenile nursery for Atlantic salmon. Circuli spacing patterns were extracted from the scales of 580 post-smolts collected in the Gulf during three seasons, 1982-1984. Post-stratification of the samples by collection date within year suggests that in some years post-smolts remain in the Gulf throughout the entire summer growth season whereas in other years only slower growing fish remain in these areas. Growth patterns for Gulf of St. Lawrence post-smolts were compared to patterns for returns from three salmon stocks from the southern end of the range in North America. These data suggest that in some years post-smolt growth in the Gulf is as robust as observed for both the one seawinter (1SW) and 2SW returns to southern rivers. Post-smolts are believed to utilize oceanic nursery areas generally; thus, comparable growth between the two stock groups suggests that the Gulf may serve as an important part of the post-smolt nursery range in some years. The conceptualization of the post-smolt nursery as a continuum between neritic and oceanic areas is essential to evaluating ocean climate and productivity effects impacting salmon recruitment.

Key Words: Atlantic salmon, circuli spacing, growth, nursery, post-smolt, survival

Introduction

Anadromous salmonids, such as Atlantic salmon (*Salmo salar*), utilize freshwater stream habitats as nursery areas for their early life history stages (Thorpe 1994). Freshwater residency provides relatively stable conditions for eggs and juvenile fish and limited spatial resoureces (Chaput et al. 1998), resulting in less annual variability in survival during the freshwater phase (Chadwick 1987). As a consequence, the relationships between spawning stock abundance and recruits migrating from freshwater take on predictable forms (Chadwick 1985; Elliott 1993). The relationships between generations of spawners, however, are not as clear due to highly variable marine survival.

The first year at sea, or the post-smolt year, for Atlantic salmon is poorly understood. The distributional behaviors of the fish at this stage appear quite variable. The transition to the marine environment is in itself a survival challenge associated with specific estuarine habitats (Levings 1994). After post-smolts make that transition they are believed to distribute widely in ocean surface waters. This belief stems from the facts that they are rarely caught in nearshore commercial fisheries and have proven difficult to capture in directed surveys. The exception has been in the Baltic area, where the spatial confines of the Baltic Sea and post-smolt recoveries in commercial fisheries have combined to produce a relative wealth of information on the distribution and survival of post-smolts in this region (Kuikka and

Salminen 1994; Eriksson 1994; Larsson 1985). The equivalent information does not exist for North Atlantic post-smolts; thus, it is critical to acquire information on the basic biology of post-smolts so that informed interpretations of the factors affecting salmon population dynamics can be made.

Recoveries of post-smolts suggest differing habitat usage and ecological roles for post-smolts on both side of the Atlantic. Recent captures of post-smolts in the Northeast Atlantic show that they are distributed over a large oceanic region by their first summer at sea (Holm et al. 1996; Shelton et al. 1997). These distribution patterns suggest post-smolts migrate to the west and may be less likely to use neritic habitats. However, in the Northwest Atlantic the few recovery data available suggest different views of which habitats represent the nursery area for post-smolts. Salmon post-smolts have been reported in estuarine waters suggesting post-smolts may orient to inshore areas (Cunjak et al. 1989; Dutil and Coutu 1988; Robitaille et al. 1986). In contrast, direct research surveys have located post-smolts in the Labrador Sea; and, tag recoveries in bird colonies have allowed indirect inference about the extent of the post-smolt migration (Reddin and Short 1991; Montevecchi et al. 1988). Recoveries of post-smolts in estuarine areas could suggest specific habitats might serve as nursery areas for post-smolts, whereas diffuse oceanic distributions suggest juveniles adapt to adult behaviors quickly and thus do not utilize specific post-smolt nursery zones.

In this paper we re-examined material collected by Dutil and Coutu (1988) with the aim of understanding the use of the Gulf of St. Lawrence by salmon post-smolts. Specifically, we collected circuli spacing data from salmon scales to address the following questions: 1) are post-smolts retained in the Gulf of St. Lawrence during the post-smolt growth season or are they transient through the area; and 2) are post-smolts recovered in the Gulf growing at comparable rates to post-smolts likely occurring elsewhere?

Material and Methods

We collected scale circuli spacing patterns representative of post-smolt growth for juvenile salmon captured in the Gulf of St. Lawrence and for three index stocks from the southern portion of the range of salmon in North America. Gulf of St. Lawrence post-smolt salmon were collected in 1982-1984 and originally reported in Dutil and Coutu (1988). These post-smolts were captured in experimental gill nets along the northwest shore of the Gulf during the months of August to 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. 1996b); 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 spacings 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 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. 2A). For fish captured as post-smolts, measurements were taken to the edge of the scale (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.

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. Return rates for the Connecticut and Penobscot stocks originally reported in Friedland et al. (1996b) are updated here. Return rates for the Saint John stock were computed similarly and are based on smolt releases of 172, 145, and 206 thousand smolts for the period 1982-1984. 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. (1996b). 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 three ways. First, data for the post-smolt scales were compared over years, 1982-1984. The spacings for the first ten circuli pairs were compared with ANOVA. This and subsequent statistical analyses were restricted to the first ten 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 10 are not well estimated. Second, for two of the seasons, 1982 and 1983, where sufficient samples of post-smolts were available, samples were post-stratified by collection date. The post-stratification was done to achieve nearly equal numbers of samples in each stratum. In 1982, three within-year strata were created: August 8 to 17 composed of 126 samples, August 18 to September 5 composed of 121 samples, and September 7 to October 18 composed of 125 samples. In 1983, two strata were created: September 24 to 30 composed of 73 samples and October 1 to 11 composed of 81 samples. Circuli spacing of the first ten circuli pairs for the post-stratified groups were compared with ANOVA. For the third 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 sea-age groups; thus, the post-smolt scale data were compared to all five other scales growth signals. The statistical comparison was simplified to a two group ANOVA, comparing circuli spacing of the first ten circuli pairs of the post-smolts to a combined sample of all the comparison stocks.

Results

Circuli spacing patterns for the post-smolt growth zones of Gulf of St. Lawrence post-smolts were significantly different for the three year classes we examined. 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 0.050 to 0.055 mm (Figure 3). However, beyond these initial pairs the spacings diverged into three distinct patterns. Spacings for fish captured in 1982 were the widest, based on the mean spacings for pairs 4-8 which averaged in excess of 0.065 mm. Circuli spacing in this same region of the scale are progressively lower for samples collected in 1983 and 1984. In 1983, most of the mean spacings do not exceed 0.060 mm and for 1984 they do not exceed 0.055 mm. ANOVA results suggest that the yearly spacings means are significantly different for all but one of the first ten spacing pairs (Table 2). The means for spacing pair number 2 is not significantly different because the rank order of the means changes between spacing pairs 1 and 3.

Within-year comparisons of samples post-stratified by collection date suggests that in one year the same group of fish were sampled during the entire growth season; whereas, in another year, the smolt assemblage changed during the sampling period. All three post-stratified groups formed from the 1982 data show a similar pattern of circuli spacing versus circuli pair through pair number 12 (Figure 4A). Spacing means for higher number pairs begin to diverge after pair 12; however, these means are estimated with low precision and reflect the lower sample sizes available to estimate the pairs. No significant differences exist between the spacing means for circuli pairs 1-10 (Table 3). In contrast, the data for 1983 show that spacing patterns and growth were different for early versus late season collections. Fish collected in September had wider circuli spacings for circuli pairs 4-10 than fish collected in October (Figure 4B). The September samples had spacings generally above 0.05 mm; whereas, the October sample was below. Most of the statistical comparisons were significant and those that were not significant at $p=0.05$ were significant at $p=0.1$ (Table 3).

Circuli spacing patterns for Gulf of St. Lawrence post-smolts were both similar and dissimilar to patterns observed for other stocks. For smolt year 1982, Gulf of St. Lawrence post-smolts, Penobscot, and Saint John returns showed similar patterns of circuli spacing versus circuli pair (Figure 5A). This comparison included both maturity groups, 1SW and 2SW returns, within stocks. The pattern for Connecticut River 2SW returns shows a different trajectory of narrower spacings with increasing circuli pair number. When compared statistically, mean spacings for Gulf post-smolts are significantly higher and lower than the mean for the three comparison stocks (Table 4). The mean spacing for circuli pair 1 is significantly lower for Gulf post-smolts than for the other stocks, but the relationship between the stocks changes with the means for pairs 4-8 as the rank order changes. The rank order changes again by circuli pair 10. In 1983, the spacing pattern for the post-smolts could not be distinguished from the combined signals for the other stocks (Figure 5B). The statistical comparison reveals no significant differences (Table 4). The Connecticut River stock had the narrowest spacings whereas the widest spacings were observed in Penobscot and St. John fish. In 1984, spacing patterns vary over an even wider range suggesting the different stocks experienced different growth regimes (Figure 5C). Mean spacings for Gulf post-smolts are significantly lower than the comparison stocks with the exception of one spacing pair (Table 4).

The three stocks provided for comparisons to Gulf of St. Lawrence 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 analysis suggests that the role of the Gulf of St. Lawrence as salmon post-smolt nursery habitat varies annually. In some years it appears that the growth of post-smolts retained in the Gulf is as robust as observed for post-smolts assumed to use open ocean habitats. This correlation suggests that either post-smolts from other areas invade the Gulf and use it as a nursery area; or, the Gulf region is continuous with a larger area of similar growth conditions where the nursery is formed. In other years it appears only the smaller, and assumed less robust, post-smolts remain in the Gulf area suggesting that the nursery was formed elsewhere.

The Gulf of St. Lawrence is a large, complex system that offers a diversity of feeding conditions to smolts upon their entrance into the marine environment. Growth rates would be expected to vary spatially in the Gulf owing to, among other things, highly variable thermal conditions over years. Nursery habitats within the Gulf appear to provide conditions that would support growth rates comparable to those observed in hatchery-reared stocks. But, what clearly differentiates the Gulf habitats from most offshore areas is the rapid continental cooling that occurs in the fall resulting in an emigration of post-smolts from the region (Dutil and Coutu 1988). The northern Gulf can cool to temperatures below 2°C by late November and to lethal temperatures later in winter from the surface to a depth of 100 m. Thus, the Gulf must be viewed as a seasonally transient habitat for post-smolts in most, if not all years.

We view nursery habitat for post-smolt salmon as being dynamically defined in that it shifts spatial location on an annual basis to regions where the production will support growth. Many marine fishes utilize staged distribution separations between estuarine, coastal, and offshore habitats (Blabber et al. 1995). North American origin salmon are generally concentrated in the Labrador Sea as feeding adults or on various migration routes back to their natal rivers as maturing fish (Reddin and Shearer 1987).

However, post-smolt distributions are regulated in part by passive displacement mechanisms and the swimming potential of the fish (Reddin and Friedland 1993). As such, post-smolt(Jonsson et al. 1993) migration routes are unlikely to be equivalent among years (Caron 1983). At some point during the post-smolt's first growing season, swimming ability begins to exceed current velocity and post-smolts can more effectively modify their distribution according to preferences driven by migration mechanisms or foraging behavior. These factors may allow post-smolt to concentrate in specific habitats that best suit their feeding requirements and afford them some measure of predation release. However, the process of habitat selection may result in a nursery that utilizes different areas each year and thus not linked to a specific area (Friedland et al. 1996a). Therefore, years of poor feeding and growth conditions in the Gulf of St. Lawrence do not preclude the use of other neritic areas as post-smolt nursery. For example, in some years the nursery may set up along the south coast of Newfoundland or make use of few neritic habitats as the fish distribute in offshore areas.

Contemporary characterizations of post-smolt populations may be inadequate if they fail to account for the distribution of post-smolts in neritic habitats. Coherence patterns in the performance of stock complexes has led investigators to search for broad-scale forcing function to explain variation in returns rate by age (Friedland et al. 1993; Friedland et al. 1998). In the Northeast Atlantic, a direct linkage between post-smolt survival and ocean climate has been reported (Friedland et al. 1998). Spring thermal condition were associated with the survival of North Sea stocks, which argues that the post-smolt nursery in that region was oceanic and thus directly affected by ocean climate change. However, interpretation of a signal for survival in the Northwest Atlantic has been complicated by the interplay of survival and maturation (Friedland et al. in press). As the search continues for factors affecting the survival of Northwest Atlantic post-smolts, investigators must be cognizant of the fact that much of the nursery may occur in neritic waters and thus not be responding solely to ocean scale phenomena. This situation may be particularly important in evaluating coastal and offshore predators and how they might be impacting salmon populations. A gannet colony may exert predation pressure over a substantial segment of the northern coast of North America; thus, these and other bird species that are adapted to surface prey such as Atlantic salmon post-smolts could cause significant impacts (Montevecchi and Myers 1997).

Our statistical comparisons of growth patterns were low-power tests and could be improved with the inclusion of growth information from stocks originating in the Gulf of Lawrence itself. We assumed that the range of growth patterns provided by the three comparison stocks is representative of stocks outside the Gulf region. However, the samples fail to account for growth signals from wild stocks and only include populations from the southern portion of the range. The strength of the sample is that it does include three stocks of varying growth and survival characteristics, thus supporting the contention it likely represents a range of growth responses.

A future challenge would be to characterize the thermal properties and production characteristics of the area potentially comprising the post-smolt nursery to evaluate its spatial and temporal extent and annual variability. From these descriptive analyses, it may be possible to design simulation and field experiments to confirm how the post-smolt nursery is formed and what driving forces affect it and post-smolts.

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Table 1

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

Stock	Age	Smolt Year 1982	1983	1984
Connecticut	2SW	52	81	110
Penobscot	1SW	65	63	57
	2SW	75	75	40
Saint John	1SW	84	65	51
	2SW	81	67	54
Gulf of St. Lawrence	Post-Smolt	372	154	54

Table 2

Results of ANOVAs testing year effect in scale circuli spacing data from collections of post-smolt salmon from the Gulf of St. Lawrence during 1982 to 1984.

Spacing Pair	Effect DF	Effect MS	Error DF	Error MS	F	p-level	
1	2	0.00291	577	0.00015	19.312	0.00	*
2	2	0.00023	577	0.00020	1.170	0.31	
3	2	0.00112	577	0.00024	4.605	0.01	*
4	2	0.00290	577	0.00021	13.491	0.00	*
5	2	0.00591	576	0.00020	28.895	0.00	*
6	2	0.00700	575	0.00017	40.579	0.00	*
7	2	0.00620	574	0.00019	33.492	0.00	*
8	2	0.00482	573	0.00015	31.914	0.00	*
9	2	0.00398	559	0.00016	24.686	0.00	*
10	2	0.00217	526	0.00016	13.521	0.00	*

Table 3

Results of ANOVAs comparing scale circuli spacing for successive time periods from collections of post-smolt salmon from the Gulf of St. Lawrence during 1982 and 1983.

Year	Spacing Pair	Effect DF	Effect MS	Error DF	Error MS	F	p-level	
1982	1	2	0.00015	369	0.00014	1.085	0.34	
	2	2	0.00008	369	0.00021	0.365	0.69	
	3	2	0.00036	369	0.00022	1.612	0.20	
	4	2	0.00013	369	0.00021	0.639	0.53	
	5	2	0.00021	369	0.00018	1.167	0.31	
	6	2	0.00002	369	0.00015	0.137	0.87	
	7	2	0.00038	368	0.00014	2.655	0.07	
	8	2	0.00003	368	0.00013	0.215	0.81	
	9	2	0.00017	355	0.00014	1.202	0.30	
	10	2	0.00027	324	0.00015	1.849	0.16	
1983	1	1	0.00001	152	0.00013	0.057	0.81	
	2	1	0.00000	152	0.00015	0.000	0.99	
	3	1	0.00014	152	0.00024	0.582	0.45	
	4	1	0.00120	152	0.00018	6.535	0.01	*
	5	1	0.00133	152	0.00024	5.424	0.02	*
	6	1	0.00129	152	0.00018	6.977	0.01	*
	7	1	0.00084	152	0.00027	3.067	0.08	
	8	1	0.00129	152	0.00019	6.713	0.01	*
	9	1	0.00064	152	0.00021	3.076	0.08	
	10	1	0.00093	152	0.00017	5.412	0.02	*

Table 4

Results of ANOVAs comparing scale circuli spacing for Gulf of St. Lawrence post-smolts and 1SW and 2SW returns to the Connecticut, Penobscot, and Sant John rivers for smolt years 1982-1984.

Year	Spacing Pair	Effect DF	Effect MS	Error DF	Error MS	F	p-level	
1982	1	1	0.00702	727	0.00015	47.053	0.00	*
	2	1	0.00057	727	0.00018	3.155	0.08	
	3	1	0.00086	727	0.00020	4.364	0.04	*
	4	1	0.00128	727	0.00018	7.165	0.01	*
	5	1	0.00425	727	0.00017	24.541	0.00	*
	6	1	0.00256	727	0.00015	16.600	0.00	*
	7	1	0.00248	726	0.00015	16.517	0.00	*
	8	1	0.00061	726	0.00015	4.086	0.04	*
	9	1	0.00001	713	0.00015	0.081	0.78	
	10	1	0.00081	682	0.00017	4.872	0.03	*
1983	1	1	0.00050	503	0.00016	3.117	0.08	
	2	1	0.00000	503	0.00019	0.004	0.95	
	3	1	0.00001	503	0.00021	0.029	0.87	
	4	1	0.00001	503	0.00023	0.032	0.86	
	5	1	0.00005	503	0.00022	0.232	0.63	
	6	1	0.00003	503	0.00020	0.156	0.69	
	7	1	0.00018	503	0.00021	0.873	0.35	
	8	1	0.00002	503	0.00018	0.093	0.76	
	9	1	0.00006	503	0.00020	0.277	0.60	
	10	1	0.00000	503	0.00020	0.002	0.97	
1984	1	1	0.00168	364	0.00018	9.118	0.00	*
	2	1	0.00125	364	0.00020	6.302	0.01	*
	3	1	0.00052	364	0.00022	2.396	0.12	
	4	1	0.00237	364	0.00020	11.568	0.00	*
	5	1	0.00336	363	0.00020	16.552	0.00	*
	6	1	0.00552	362	0.00022	25.136	0.00	*
	7	1	0.00551	362	0.00015	35.738	0.00	*
	8	1	0.00606	361	0.00016	39.032	0.00	*
	9	1	0.00783	360	0.00016	48.985	0.00	*
	10	1	0.00512	358	0.00017	31.024	0.00	*

Table 5

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

Smolt	Connecticut		Penobscot			Saint John		
Year	2SW	Fraction	1SW	2SW	Fraction	1SW	2SW	Fraction
1982	0.03	0.00	0.05	0.42	0.08	0.91	0.65	0.49
1983	0.30	0.02	0.05	0.66	0.06	1.00	0.61	0.54
1984	0.09	0.00	0.04	0.59	0.04	0.98	0.39	0.59
Mean	0.13	0.01	0.09	0.47	0.12	1.47	0.57	0.59

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Figure 1

Map of Northwest Atlantic area showing post-smolt habitat for stocks in the Gulf of St. Lawrence and south (horizontal hatching) and sampling area for Gulf of St. Lawrence post-smolts (vertical hatching).

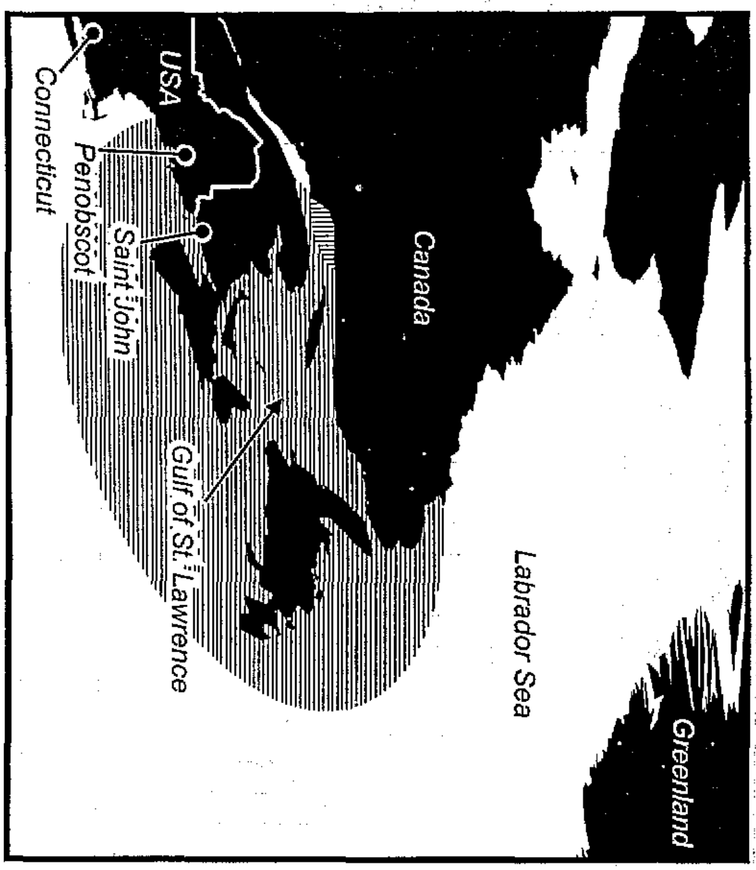

Figure 2

Illustrations of Atlantic salmon scale from a 1SW salmon (A) and a post-smolt salmon (B). Focus of each scale is marked; freshwater growth zone extends from focus to start of marine growth; and, post-smolt growth zone extends to first winter annuli. The figures are not in scale.

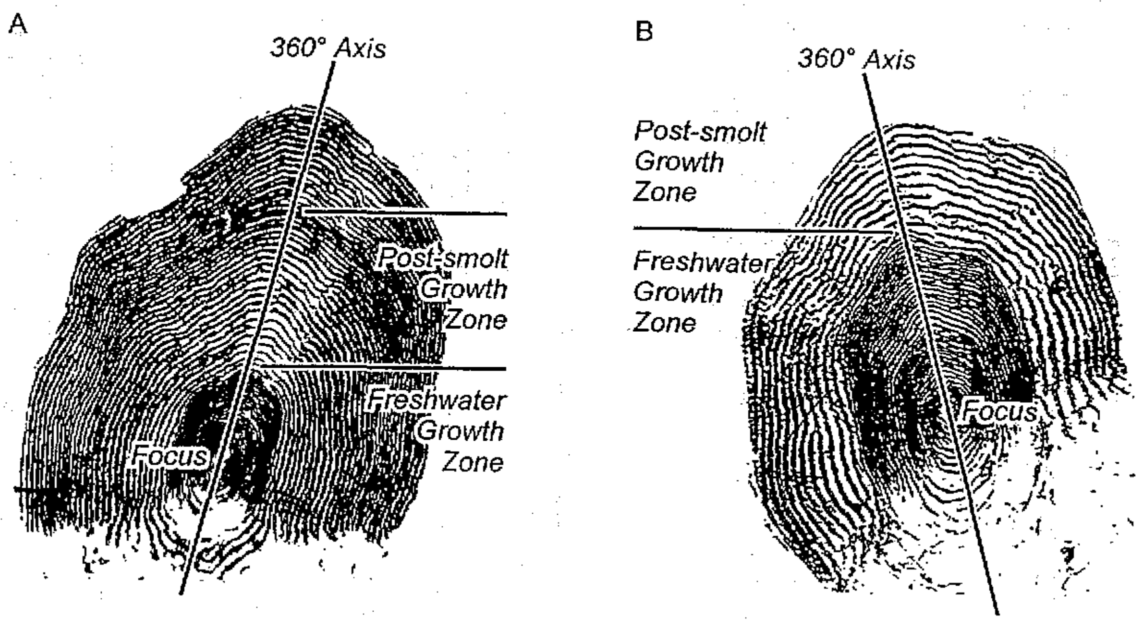

Figure 3

Circuli spacing versus circuli pair for Gulf of St. Lawrence post-smolts for three smolt year classes, 1982-1984. Error bars mark 95% confidence intervals.

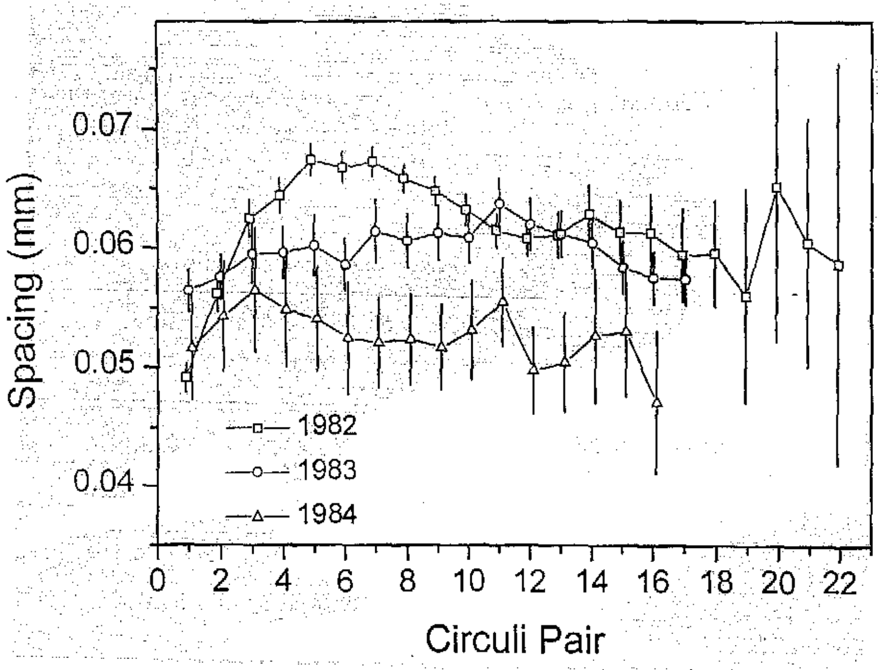

Figure 4

Circuli spacing versus circuli pair for Gulf of St. Lawrence post-smolts for two smolt year classes, 1982 (A) and 1983 (B). Samples post-stratified by date of capture. Error bars mark 95% confidence intervals.

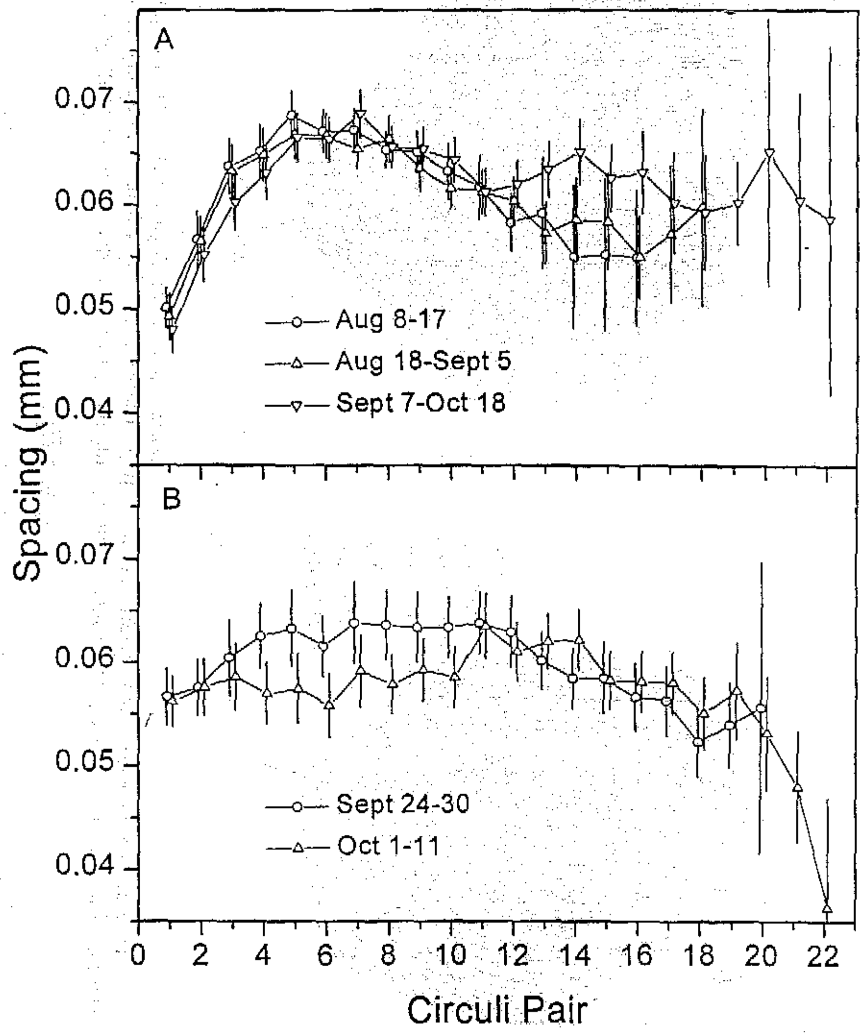

Figure 5

Circuli spacing versus circuli pair for Connecticut 2SW (Conn), Penobscot 1SW and 2SW (Pen), Saint John 1SW annd 2SW (SJ), and Gulf of St. Lawrence post-smolts (Gulf) for three smolt year classes, 1982 (A), 1983 (B), and 1984 (C). Error bars mark 95% confidence intervals.