

Abstract.—We examined scale samples from historical collections of postsmolts from the Gulf of St. Lawrence, Canada, with the aim of understanding the role of estuarine and coastal habitats as a juvenile nursery for Atlantic salmon. Circuli spacing patterns were extracted from the scales of 580 postsmolts collected in the Gulf during three seasons, 1982–84. Poststratification of the samples by collection date within year suggests that in some years postsmolts 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 postsmolts were compared with patterns for returns from three salmon stocks from the southern end of the range in North America. These data suggest that in some years postsmolt growth in the Gulf is as robust as that observed for both the one seawinter (1SW) and two seawinter (2SW) returns to southern rivers. Postsmolts are believed to use oceanic nursery areas generally; thus, comparable growth between the two stock groups suggests that the Gulf may serve as an important part of the postsmolt nursery range in some years. The concept of the postsmolt nursery as a continuum between neritic and oceanic areas is essential to evaluating ocean climate and productivity effects on salmonid recruitment.

Growth patterns in postsmolts and the nature of the marine juvenile nursery for Atlantic salmon, *Salmo salar*

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Anadromous salmonids, such as Atlantic salmon, *Salmo salar*, use freshwater stream habitats as nursery areas for their early life history stages (Thorpe, 1994). Freshwater residency provides refuge from potential predators and relatively stable survival conditions for eggs and juveniles (Chaput et al., 1998). Thus, the recruitment of smolts during the freshwater phase is characterized by relatively low annual variability, most of which is attributed to the size of spawning escapements (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 owing to highly variable rates of marine survival.

The first year at sea, or the postsmolt year, for Atlantic salmon is poorly understood. The transition to the marine environment is in itself a survival challenge associated with specific estuarine habitats (Levings, 1994). After postsmolts make the

transition, they are believed to disperse widely in ocean surface waters. This belief stems from the facts that they are rarely caught in near-shore fishing gears 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 postsmolt recoveries in commercial fisheries have combined to produce a relative wealth of information on the distribution and survival of postsmolts in that region (Larsson, 1985; Eriksson 1994; Kuikka and Salminen 1994). The equivalent information does not exist for North Atlantic postsmolts; thus, it is critical to learn more about the basic biology of postsmolts so that informed interpretations of the patterns in salmonid population dynamics can be made.

Recoveries of North American versus European postsmolts suggest that habitat use and ecological roles may differ for the early marine stages of the two stock complexes. Recent captures of postsmolts 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 that postsmolts migrate to the northwest and may be less likely to use inshore neritic habitats. However, in the Northwest Atlantic, the few recovery data available for postsmolts suggest differing views of which habitats represent the nursery area for postsmolts. Salmon postsmolts have been reported to use estuarine waters; therefore it is possible that they possess specific behaviors to orient themselves to inshore areas during their first year at sea (Robitaille et al., 1986; Dutil and Coutu, 1988; Cunjak et al., 1989). In contrast, postsmolts have also been collected from research surveys in the Labrador Sea and indirectly from bird colonies, providing evidence that the extent of the postsmolt migration includes waters north of Newfoundland (Montevecchi et al., 1988; Reddin and Short, 1991). Recoveries of postsmolts in estuarine areas support the hypothesis that specific habitats serve as nursery areas for postsmolts, whereas recoveries in the pelagic zone support the alternative, that juveniles have thermal preferences similar to adults and do not use specific postsmolt nursery areas.

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 postsmolts. Specifically, we collected circuli spacing data from salmon scales to address the following questions: 1) Are postsmolts retained in the Gulf of St. Lawrence during the postsmolt growth season or are they transient in the area?; and 2) Do postsmolts recovered in the Gulf exhibit growth patterns similar to postsmolts from other stocks? The answers to these questions will hopefully allow us to make some inference about the nature of the nursery for Atlantic salmon and salmonids in general.

Material and methods

We collected scale circuli spacing data representative of postsmolt 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 postsmolt salmon were collected in 1982–84 and were originally reported in Dutil and Coutu (1988). These postsmolts were captured in experimental gill nets along the northwest shore of the Gulf during the months from

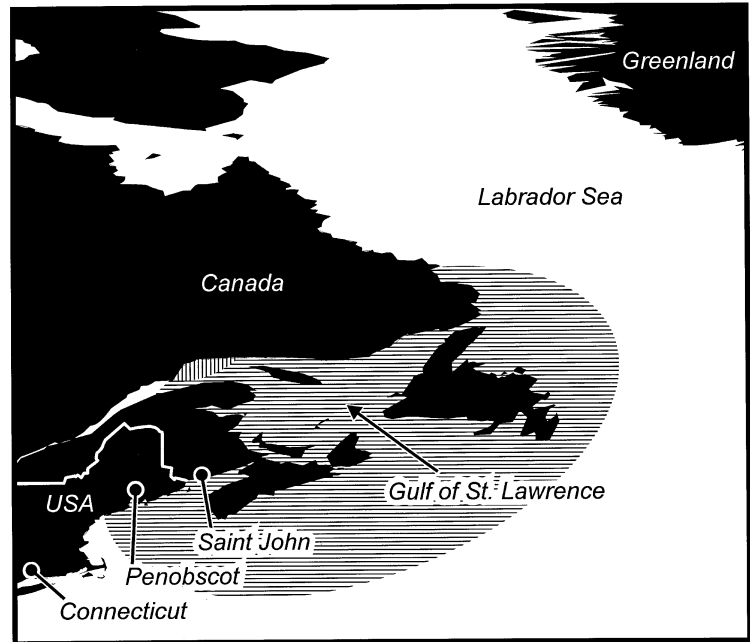


Figure 1

Map of Northwest Atlantic area showing postsmolt habitat for stocks in the Gulf of St. Lawrence and south (horizontal hatching) and sampling area for Gulf of St. Lawrence postsmolts (vertical hatching).

Table 1

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

Stock	Age	Smolt year		
		1982	1983	1984
Connecticut	2SW	52	81	110
	1SW	65	63	57
Penobscot	2SW	75	75	40
	1SW	84	65	51
St. John	2SW	81	67	54
	Post smolt	372	154	54

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). Data for the Connecticut and Penobscot rivers have been presented earlier (Friedland et al., 1996b); whereas, the Saint John data are 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 inclusion in our study.

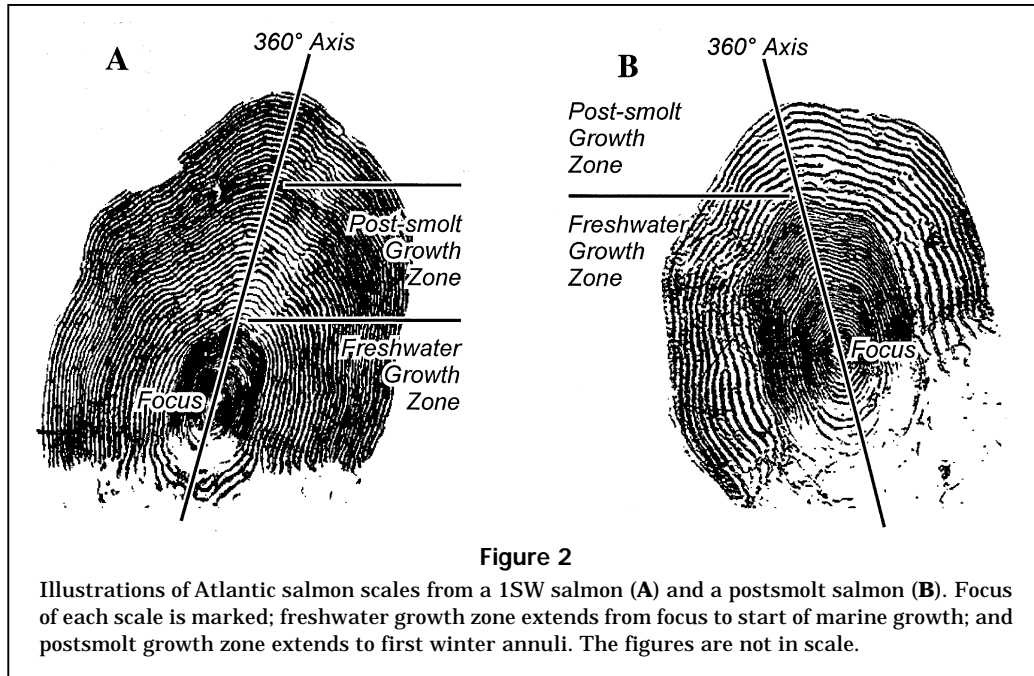


Figure 2

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

Postsmolt growth was interpreted from circuli spacing patterns deposited during the postsmolt year. Scales were cleaned and mounted between glass slides and the spacings of scale circuli were measured with a Bioscan Optimas image processing system. The first spacing was measured between the first circulus of the postsmolt growth zone and the next circulus and continued with successive circuli pairs. For maturing fish returning to their natal river after at least one winter at sea, the measurements were made through the first seawinter annulus of the scale and thus captured the entire postsmolt growth zone (Fig. 2A). For fish captured as postsmolts, measurements were taken to the edge of the scale (Fig. 2B). Thus, only part of the data collected from maturing fish was needed for comparison with the postsmolts. 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 years 1982–84, respectively. Releases over the period 1974–92 averaged approximately 200 thousand smolts annually in the Saint John system. The

fraction of the smolt cohort maturing after one seawinter, the 1SW fraction, was computed with the formulae of Friedland et al. (1996b). Likewise, these data are updated for the Connecticut and Penobscot stocks and are newly reported for the Saint John stock.

Circuli spacing data for Gulf of St. Lawrence postsmolts were compared in three ways. In the first comparison, data for the postsmolt scales were compared for the period 1982–84. The spacings of the first ten circuli pairs were compared with ANOVA. This and subsequent statistical analyses were restricted to the first ten circuli pairs because most postsmolt scales did not have circuli beyond the tenth pair. As a consequence, spacing patterns for circuli pairs beyond pair number 10 were not well estimated. In the second comparison, for two of the seasons, 1982 and 1983, where sufficient samples of postsmolts were available, samples were poststratified by collection date. The poststratification was done to achieve nearly equal numbers of samples in each stratum. In 1982, three within-year strata were created: 8 to 17 August composed of 126 samples, 18 August to 5 September composed of 121 samples, and 7 September to 18 October composed of 125 samples. In 1983, two strata were created: 24 to 30 September composed of 73 samples and 1 to 11 October composed of 81 samples. Circuli spacing of the first ten circuli pairs for the poststratified groups were compared with ANOVA. For the third comparison, circuli spacing data from Gulf postsmolt scales were compared with the circuli spacing data for the three

Table 2

Results of ANOVAs testing year effect in scale circuli spacing from collections of postsmolt salmon from the Gulf of St. Lawrence from 1982 to 1984.

Spacing pair	df effect	MS effect	df error	MS error	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	*

comparison stocks. The data for the comparison stocks were grouped by sea-age; thus, the postsmolt scale data were compared with a total of five scale growth signals. The statistical comparison was simplified to a two-group ANOVA, namely to comparing circuli spacing of the first ten circuli pairs of the postsmolts with a combined sample of all the comparison stocks.

Results

Circuli spacing patterns for the postsmolt growth zones of Gulf of St. Lawrence postsmolts 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 (Fig. 3). However, beyond these initial pairs the spacings diverged into three distinct patterns. Spacings for fish captured in 1982, based on the mean spacings for pairs 4–8, were the widest, generally larger than 0.065 mm. Circuli spacings in the same region of the scale were progressively smaller for samples collected in 1983 and 1984. In 1983, most of the mean spacings did not exceed 0.060 mm and for 1984 they did not exceed 0.055 mm. ANOVA results show that the yearly spacings means were 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.

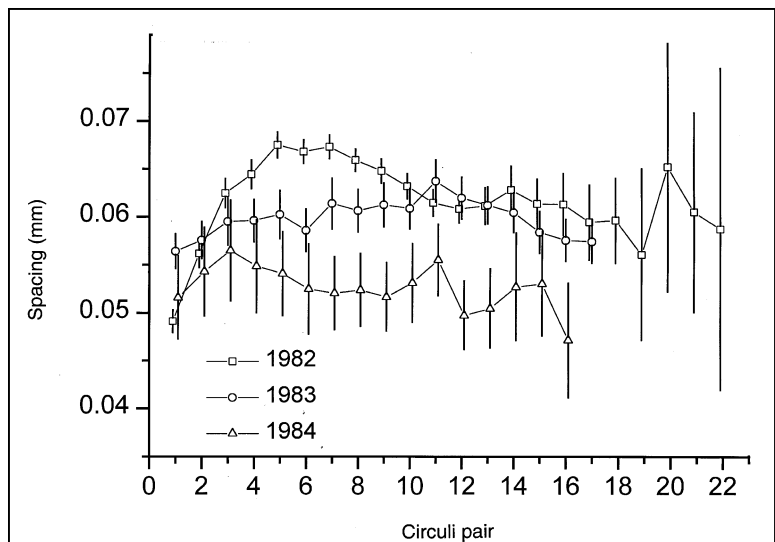


Figure 3

Circuli spacing versus circuli pair for Gulf of St. Lawrence postsmolts for three smolt year classes, 1982–84. Error bars mark 95% confidence intervals.

Within-year comparisons of Gulf of St. Lawrence samples poststratified by collection date suggest that in one year the same group or population of fish were sampled during the entire growth season; whereas, in another year, the postsmolt assemblage appeared to change during the sampling period. All three poststratified groups formed from the 1982 data showed a similar pattern of circuli spacing versus circuli pair through pair number 12 (Fig. 4A). After circuli pair 12, the mean spacing for the three poststratified groups began to diverge; however, the mean spacing for these circuli pairs was estimated

with low precision owing to the small sample sizes available. No significant differences existed between the spacing means for circuli pairs 1–10 (Table 3). In contrast, the data for 1983 showed 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 (Fig. 4B). The September samples had mean spacings generally above 0.0625 mm; whereas, the October samples had mean spacings generally below 0.06 mm. Most of the statistical comparisons between the poststratified groups were significant at either $P=0.05$ or $P=0.1$ (Table 3).

The seasonal pattern in circuli spacing for Gulf of St. Lawrence postsmolts was similar to the patterns observed for the some of the comparison stocks by year, and dissimilar in other cases. For smolt year 1982, Gulf of St. Lawrence postsmolts and Penobscot and Saint John returns showed similar seasonal patterns of circuli spacing versus circuli pair (Fig. 5A).

This comparison included both the 1SW and 2SW maturity groups within a stock. The pattern of mean circuli spacing for Connecticut River 2SW returns was different from that for the other stocks and showed an ontogenetic trajectory of narrower spacings with age. When compared statistically, mean spacings for Gulf postsmolts were significantly higher and lower than the mean for the three comparison stocks (Table 4). The mean spacing for circuli pair 1 was significantly lower for Gulf postsmolts compared with the other stocks, but the relationship between stock circuli spacing changed for pairs 4–8 as the rank order changed. The rank order changed again by circuli pair 10. In 1983, the spacing pattern for the postsmolts could not be distinguished graphically from the combined signals for the other stocks (Fig. 5B), which is supported by statistical comparison as well (Table 4). Again, the Connecticut River stock had the narrowest spacings, whereas the widest spacings were observed in Penobscot and Saint John fish.

In 1984, mean circuli spacing varied over a wide range, suggesting the different stocks experienced different growth regimes that year (Fig. 5C). What is particularly striking is that the wild-origin postsmolts from the Gulf had the narrowest mean spacings for most of the post-smolt growth season. Mean spacings for Gulf postsmolts were significantly lower than those for the comparison stocks with the exception of only one spacing pair (Table 4).

The three stocks provided for comparisons with Gulf of St. Lawrence postsmolts displayed a range of return rates and 1SW fraction, reflecting differences in survival and maturity rates. For the Connecticut stock, return rates 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 matured at 1SW. The Saint John stock had the highest return rates and the 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 stock is similar to that observed for the Penobscot stock. Thus, the Connecticut stock had the lowest survival rate and produced few early maturing fish; the Saint John stock had the highest survival rate and pro-

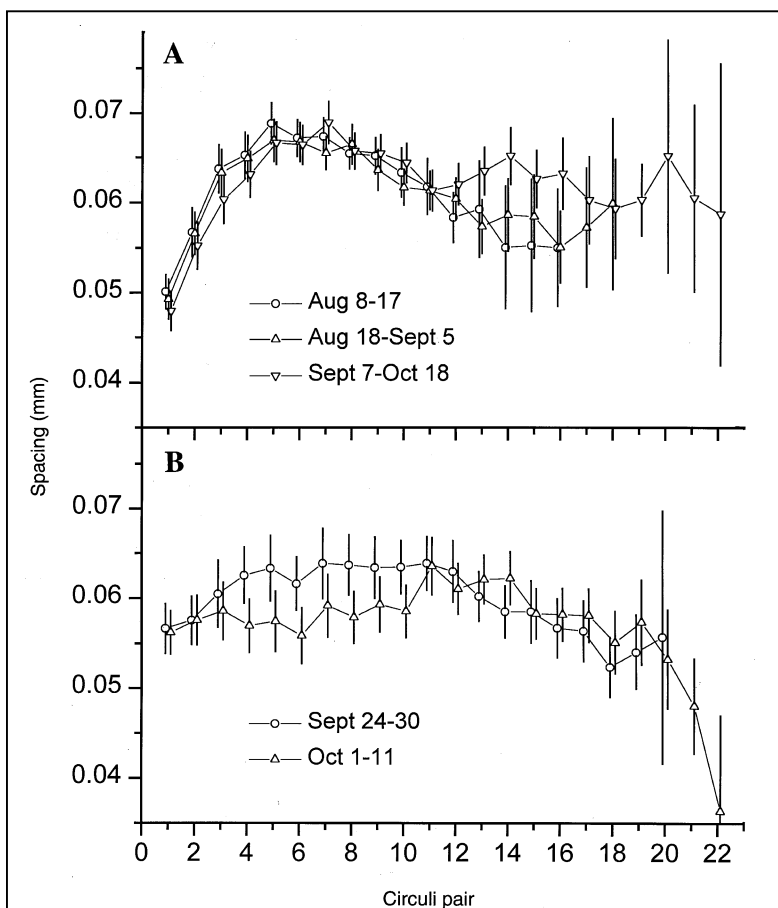


Figure 4

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

duced 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 postsmolt nursery habitat varies annually. In some years it appears that the growth of wild postsmolts retained in the Gulf is as robust as and patterned similarly to growth observed for hatchery-origin postsmolts assumed to use open ocean habitats (Reddin and Short, 1991). This correlation suggests that either postsmolts 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 that only smaller, and presumably less robust, postsmolts remain in the Gulf area and that the nursery was formed elsewhere. Variation in the suitability of nursery habitat must interact with the ability of postsmolts to migrate successfully to more favorable areas. In what was first investigated as a mechanism controlling the return migration of adults, Groot and Cooke (1987) described an analogous situation with the dis-

tribution of juvenile sockeye salmon in the Strait of Georgia. It would appear that the dominant wind patterns in the Strait can alter the annual migration of postsmolt sockeye salmon and place them in different nursery areas each year (Peterman et al., 1994). Atlantic salmon postsmolt migration trajectories may be similarly affected. In some years, postsmolts are deposited in areas like the Gulf of St. Lawrence and growth conditions are favorable enough to retain them in the region for the entire season. In other years they are not deposited or retained in the same area. Regardless, our focus shifts to the factors controlling migration and whether they covary with the factors controlling survival.

We view nursery habitat for postsmolt salmon as being dynamically defined because it shifts spatial location on an annual basis to regions where the production will support growth. Many marine fishes use 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, postsmolt distributions are regulated in part by passive displacement mechanisms and the swim-

Table 3

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

Year	Spacing pair	df effect	MS effect	df error	MS error	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 *

ming potential of the fish (Reddin and Friedland, 1993). As such, postsmolt migration routes are unlikely to be equivalent among years (Caron, 1983; Jonsson et al., 1993). At some point during the postsmolt's first growing season, swimming ability begins to exceed current velocity and postsmolts can more effectively modify their distribution according to preferences driven by migration mechanisms or foraging behavior. These factors may allow postsmolts to concentrate in specific habitats that best suit their feeding requirements and afford them some measure of protection from predation. However, the process of habitat selection may result in a nursery that encompasses 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 necessarily mean poor survival conditions because they do not preclude the use of other neritic areas as postsmolt nursery. For example, in some years the nursery may form along the south coast of Newfoundland or for that matter make use of few neritic habitats as the fish distribute in offshore areas.

Contemporary characterizations of postsmolt populations may be inadequate if they fail to account for the distribution of postsmolts in neritic habitats. Coherence patterns in the performance of stock complexes has led investigators to search for broad-scale forcing functions to explain variation in returns rate by age (Friedland et al., 1993; Friedland et al., 1998a). In the Northeast Atlantic, a direct link between postsmolt survival and ocean climate has been reported (Friedland et al., 1998a). Spring thermal conditions were associated with the survival of North Sea stocks, which argues that the postsmolt nursery in that region was oceanic and thus directly affected by ocean climate change. However, interpretation of survival signals in the Northwest Atlantic has been complicated by the interplay of mortality and maturation (Friedland et al., 1998b). As the search continues for the factors affecting the survival of Northwest Atlantic postsmolts, investigators must be cognizant of the fact that much of the nursery may occur in inshore neritic waters rather than in pelagic ecosystems and thus may not respond solely to ocean-scale phenomena. This situation may be particularly important in evaluating coastal and offshore predators and how

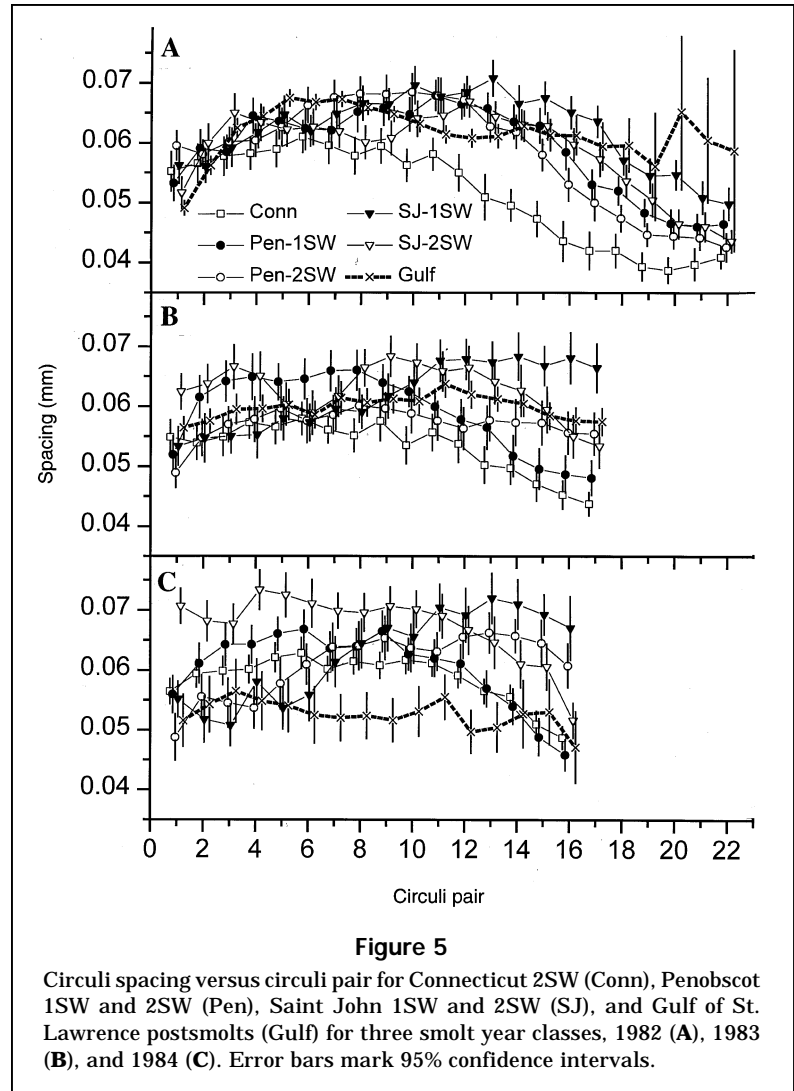


Figure 5

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

they might be impacting salmon populations. For example, a gannet colony may exert predation pressure over a substantial part of the northern coast of North America; thus, these and other bird species that are adapted to surface prey, such as Atlantic salmon postsmolts, could cause significant predation (Montevecchi and Myers, 1997).

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 postsmolts from

Table 4

Results of ANOVAs comparing scale circuli spacing for Gulf of St. Lawrence postsmolts and 1SW and 2SW returns to the Connecticut, Penobscot, and St. John rivers for smolt years 1982–84.

Year	Spacing pair	df effect	MS effect	df error	MS error	<i>F</i>	<i>P</i> -level	
1982	1	1	0.00702	727	0.00015	47.053	0.000	*
	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	0.00327	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 1974–92.

Smolt year	Connecticut		Penobscot			St. John		
	2SW	Fraction	1SW	2SW	Fraction	1SW	2SW	Fraction
1982	0.02	0.00	0.05	0.52	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

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 postsmolts in most, if not all, years.

Our comparisons of growth patterns could be enhanced with the inclusion of growth information from stocks originating in the Gulf of St. 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 failed to account for growth signals from wild stocks and included only populations from the southern portion of the range. However, the strength of the sample is that it did include three stocks of varying growth and survival characteristics, thus supporting the contention that it likely represents a range of growth responses similar to those occurring in wild stocks.

A future challenge for research would be to characterize the thermal properties and production characteristics of the area potentially comprising the postsmolt nursery to evaluate its spatial and temporal extent and annual variability. From these descriptive analyses, it may be possible to design migration simulations and field experiments that could begin to describe the mechanisms that form the postsmolt nursery and, in turn, it may be possible to develop an understanding of the factors affecting postsmolt survival and recruitment in salmonid populations.

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Literature cited

- Blabber, S. J. M., D. T. Brewer, and J. P. Salini.**
1995. Fish communities and the nursery role of shallow inshore water of a tropical bay in the Gulf of Carpentaria, Australia. *Estuarine Coastal Shelf Sci.* 40(2):177-93.
- Caron, F.**
1983. Migration toward the Atlantic of postsmolt (*Salmo salar*) from the Gulf of St. Lawrence. *Nat. Can.* 110(2):223-227.
- Chadwick, E. M. P.**
1985. The influence of spawning stock on production and yield of Atlantic salmon, *Salmo salar* L., in Canadian rivers. *Aquacult. Fish. Manage.* 16(1):111-719.
1987. Causes of variable recruitment in a small Atlantic salmon stock. *Am. Fish. Soc. Symp. Ser.* 1:390-401.
- Chaput, G., J. Allard, F. Caron, J. B. Dempson, C. C. Mullins, and M. F. O'Connell.**
1998. River-specific target spawning requirements for Atlantic salmon (*Salmo salar*) based on a generalized smolt production model. *Can. J. Fish. Aquat. Sci.* 55:246-61.
- Cunjak, R. A., E. M. P. Chadwick, and M. Shears.**
1989. Downstream movements and estuarine residence by Atlantic salmon parr (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 46(9):1466-1471.
- Dutil, J.-D., and J.-M. Coutu.**
1988. Early marine life of Atlantic salmon, *Salmo salar*, post-smolts in the northern Gulf of St. Lawrence. *Fish. Bull.* 86(2):197-212.
- Elliott, J. M.**
1993. A 25-year study of production of juvenile sea-trout, *Salmo trutta*, in an English Lake District stream. *Can. Spec. Publ. Fish. Aquat. Sci.* 118:109-22.
- Eriksson, T.**
1994. Mortality risks of Baltic salmon during downstream migration and early sea-phase: effects of body size and season. *Nord. J. Freshwater Res.* 69:100.
- Friedland, K. D., D. W. Ahrenholz, and J. F. Guthrie.**
1996a. Formation and seasonal evolution of Atlantic menhaden juvenile nurseries in coastal estuaries. *Estuaries* 19(1):105-114.
- Friedland, K. D., R. E. Haas, and T. F. Sheehan.**
1996b. Postsmolt growth, maturation, and survival of two stocks of Atlantic salmon. *Fish. Bull.* 94(4):654-63.
- Friedland, K. D., L. P. Hansen, and D. A. Dunkley.**
1998a. Marine temperatures experienced by postsmolts and the survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area. *Fish. Oceanogr.* 7:22-34.
- Friedland, K. D., D. G. Reddin, and J. F. Kocik.**
1993. Marine survival of North American and European Atlantic salmon: effects of growth and environment. *ICES J. Mar. Sci.* 50:481-92.
- Friedland, K. D., D. G. Reddin, N. Shimizu, R. E. Haas, and A. F. Youngson.**
1998b. Strontium:calcium ratios in Atlantic salmon otoliths and observations on growth and maturation. *Can. J. Fish. Aquat. Sci.* 55:1158-1168.
- Groot, C., and K. Cooke.**
1987. Are the migrations of juvenile and adult Fraser River sockeye salmon (*Oncorhynchus nerka*) in near-shore waters related? *Can. Spec. Publ. Fish. Aquat. Sci.* 96:53-60.
- Holm, M., J. Holst, and L. Hansen.**
1996. Atlantic salmon surveys in the Norwegian Sea from July 1991-August 1995. *Aquaculture* 1996(1):21.
- Jonsson, N., L. P. Hansen, and B. Jonsson.**
1993. Migratory behavior and growth of hatchery-reared postsmolt Atlantic salmon *Salmo salar*. *J. Fish Biol.* 42:435-443.
- Kuikka, S., and M. Salminen.**
1994. Dependency of stocking result on the size of the released salmon smolts (*Salmo salar* L.) in the northern part of the Baltic Sea. *Nord. J. Freshwater Res.* 69:99.
- Larsson, P.-O.**
1985. Predation on migrating smolt as a regulating factor in Baltic salmon, *Salmo salar* L., populations. *J. Fish Biol.* 26(4):391-397.
- Levings, C. D.**
1994. Feeding behavior of juvenile salmon and significance of habitat during estuary and early sea phase. *Nord. J. Freshwater Res.* 69:7-16.

Montevecchi, W. A., D. K. Cairns, and V. L. Birt.

1988. Migration of postsmolt Atlantic salmon, *Salmo salar*, off northeastern Newfoundland, as inferred by tag recoveries in a seabird colony. *Can. J. Fish. Aquat. Sci.* 45(3): 568–71.

Montevecchi, W. A., and R. A. Myers.

1997. Centennial and decadal oceanographic influences on changes in northern gannet populations and diets in the north-east Atlantic: implications for climate change. *ICES Journal of Marine Science* 54:608–14.

Peterman, R. M., S. G. Marinone, K. A. Thomson, I. D. Jardine, R. N. Crittenden, P. H. Leblond, and C. J. Walters.

1994. Simulation of juvenile sockeye salmon (*Oncorhynchus nerka*) migrations in the Strait of Georgia, British Columbia. *Fish. Oceanogr.* 3(4):221–35.

Reddin, D. G., and K. D. Friedland.

1993. Marine environmental factors influencing the movement and survival of Atlantic salmon. In D. Mills (ed.), *salmon in the sea*, p. 79–193. Fishing News Books, London.

Reddin, D. G., and W. M. Shearer.

1987. Sea-surface temperature and distribution of Atlantic salmon in the Northwest Atlantic Ocean. *Am. Fish. Soc. Symp. Ser.* 1:262–75.

Reddin, D. G., and P. B. Short.

1991. Postsmolt Atlantic salmon (*Salmo salar*) in the Labrador Sea. *Can. J. Fish. Aquat. Sci.* 48(1):2–6.

Robitaille, J. A., Y. Cote, G. Shooner, and G. Hayeur.

1986. Growth and maturation patterns of Atlantic salmon, *Salmo salar*, in the Koksoak River, Ungava, Quebec. In D. J. Meerburg (ed.), *Salmonid age at maturity*, p. 62–69. *Can. Spec. Publ. Fish. Aquat. Sci.* 89.

Shelton, R. G. J., W. R. Turrell, A. MacDonald, I. S. McLaren, and N. T. Nocoll.

1997. Records of postsmolt Atlantic salmon, *Salmo salar* L., in the Faroe-Shetland Channel in June 1996. *Fisheries Research (Amsterdam)* 31(1–2):159–62.

Thorpe, J.

1994. Salmonid fishes and the estuarine environment. *Aquaculture* 17(1A):76–93.