Abstract.—Marine survival and sea-age at maturity of two hatchery-dependent stocks of Atlantic salmon were compared in respect to differences in post-smolt growth as evidenced by the circuli spacing patterns of their scales. The two stocks, the Penobscot and Connecticut, are located at the southern extent of the range of Atlantic salmon in North America. Return rates for 1SW (one seawinter) and 2SW salmon and the fraction of the smolt year class or cohort that matured as 1SW fish were found to be significantly higher for the Penobscot stock. Using image processing techniques, we extracted intercirculi distances from scales of 2,302 2SW fish. Circuli spacing data were expressed as growth indices for spring (when post-smolts first enter the ocean), summer (when growth appears maximal), and winter (when growth appears to be at a minimum). Circuli spacings of the Penobscot fish were wider during the summer season than were those for conspecifics from the Connecticut River of the same smolt year class. The results suggest that post-smolt growth may play a significant role in deciding age at maturity and survival patterns for Atlantic salmon stocks.

Post-smolt growth, maturation, and survival of two stocks of Atlantic salmon

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Variation in the marine survival and sea-age of maturation of individual Atlantic salmon stocks, *Salmo salar* L., has ramifications for the management of these stocks in both freshwater and marine environments. Mixed-stock fisheries for salmon indiscriminately harvest stocks of varying productivity, often leading to the over harvesting of weaker stocks even when exploitation is at a level considered safe for the stock complex (Ricker, 1958). Homewater or terminal fisheries can also over harvest weak stocks when shifts in age at maturity and survival occur (Minard and Meacham, 1987). Understanding these periods of changing stock dynamics will help to ensure that management measures are taken to protect the stocks and enhance the fishery.

Events during the post-smolt year are critical to the survival and maturation of Atlantic salmon (Mills, 1989; Salminen et al., 1995); however, the factors shaping salmon population abundances during this period are poorly known (Friedland et al., 1993). Many sources of mortality, such as predation, disease, and parasitism, affect young salmon during their first year at sea. The effect of these sources of mortality is to some extent influenced by the size and condition of the post-smolts; thus, their effect would be expected to vary between years and among stocks (Mathews and Ishida, 1989; Holtby et al. 1990; Salminen et al., 1995). For example, predation during the post-smolt year may determine overall survivorship in salmon, but it is not known how much of the predation on young salmon is controlled by predator abundance versus the size and growth of the post-smolts themselves (Hislop and Shelton, 1993; Hargreaves, 1994). Predation theory suggests that the probability of survival for an individual increases considerably as its body size exceeds sizes vulnerable to potential predators (Werner and Hall, 1974; Mikheev, 1984; L'Abee-Lund et al., 1993). If juveniles remain in a developmental stage that makes them vulnerable to mortality, cumulative mortality will increase (Cushing, 1975). If a stock experiences depressed post-smolt growth, it may be susceptible to high mortality for a longer time compared with other stocks exploiting the same feeding area. Likewise, similar growth-mediated mechanisms can be envisioned for other sources of mortality such as diseases and parasitism.

The onset of sexual maturation in fishes is an inherited trait that operates within a range of phenotypic

plasticity (Via and Lande, 1985; Saunders, 1986; Stearns, 1992; Scheiner 1993; Trippel, 1995). Growth and environment during the post-smolt period play an important role in influencing the sea-age at maturation of salmon (Scarnecchia, 1983; Martin and Mitchell, 1985; Neilson and Geen, 1986; L'Abee-Lund, 1989; Scarnecchia et al., 1989; Skilbrei, 1989). Friedland and Haas (1996) found that summer post-smolt growth was positively correlated with maturation, suggesting that physical readiness to mature may be achieved during the summer period. Examining post-smolt growth in stocks with differing maturation rates should provide new insights into the mechanisms controlling salmon maturation.

In this study, we compare the marine survival and age at maturity of two hatchery dependent stocks of Atlantic salmon. We also describe and analyze circuli spacing and other length measurements from the scales of two seawinter returns to characterize growth during the post-smolt phase and to examine the role of post-smolt growth in affecting survival and maturation.

Materials and methods

Return rate and cohort age at maturity

Return rate by individual sea-age and cohort sea-age at maturity were calculated for two Atlantic salmon stocks, the hatchery components of the salmon runs in the Penobscot and Connecticut rivers in the United States. These rivers are situated at the southern end of the range of Atlantic salmon in North America (Fig. 1). Salmon from these rivers migrate to feeding areas as distant as the Labrador Sea. We analyzed data from 1977 to 1990, a period during which smolt releases in the Penobscot River ranged from 200,000 to 687,000 fish per year and in the Connecticut River from 32,000 to 476,000 fish per year (Table 1). Early in the time series, releases in both rivers were mostly two-year-old smolts, whereas in recent years, most of the releases have been yearlings. Freshwater returns of both 1SW (one seawinter) and 2SW salmon were ascertained from fishway trap counts and from recreational catches in the Penobscot River, as well as from trap counts in the Connecticut River (no legal Atlantic salmon fishery exists for this river). Return rates were calculated as simple ratios, expressed as returns per 1,000 smolts released.

The fraction of a cohort or smolt year class that matured after only a single winter at sea was derived by using both counts of adult returns by sea-age and fishing mortality that impacted the cohort.
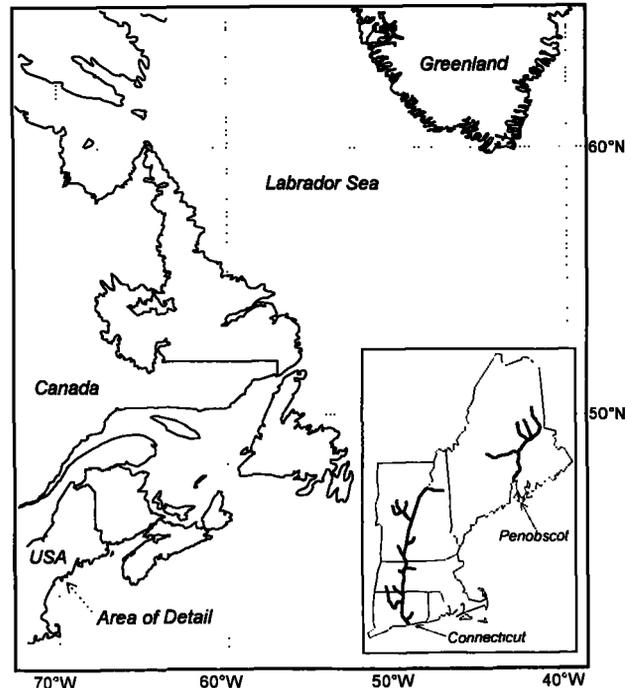

Figure 1

Map of the northwest Atlantic Ocean with detail showing location of the Penobscot and Connecticut rivers.

Fish from the Penobscot and Connecticut rivers were exploited in marine fisheries in Canada and Greenland during the study period. To account for this, we applied annual instantaneous fishing mortality rates (F in Table 1) for North American fish that were maturing as 2SW salmon (Friedland and Haas, 1996).

The observed return of 1SW salmon to freshwater (R_1) is the product of the maturation fraction (Ψ) and the size of the cohort immediately before the 1SW fish return to homewaters and the 1SW fisheries have commenced (N_0). Because we were modeling the cohort split immediately before the 1SW runs occur, natural mortality for this fraction of the cohort (M_1) was zero.

$$R_1 = N_0 * \Psi * \exp^{-M_1}. \tag{1}$$

The observed return of 2SW salmon (R_2) is assumed to be the remainder of the cohort that did not mature as 1SW fish and that survived for an additional 10 months at sea, plus the mortality associated with fishing (M_2=0.1 is from Friedland and Haas, 1996, and F is given in Table 1). The additional time 2SW salmon stay at sea is assumed to be 10 months, as opposed to one year, because 2SW salmon usually return to the river earlier in the year than 1SW fish.

Table 1

Smolt releases (number), returns (number), return rates by sea-age (‰), and 1SW fraction (Ψ) for the Penobscot (Pen) and Connecticut (Conn) Atlantic salmon stocks.

Smolt year	Smolt release Pen	Smolt release Conn	Yearling smolts % Pen	Yearling smolts % Conn	1SW returns Pen Return	1SW returns Pen Rate	1SW returns Conn Return	1SW returns Conn Rate	2SW returns Pen Return	2SW returns Pen Rate	2SW returns Conn Return	2SW returns Conn Rate	Fishing mortality	1SW fraction Pen	1SW fraction Conn
1977	388,500	96,400	34	0	123	0.36	3	0.03	671	1.98	50	0.52	0.511	0.091	0.032
1978	202,500	32,100	30	0	203	1.00	4	0.12	2,570	12.69	164	5.11	0.356	0.048	0.015
1979	296,300	124,900	17	0	652	2.20	4	0.03	2,454	8.28	513	4.11	0.433	0.135	0.005
1980	584,600	51,800	63	0	888	1.52	6	0.12	3,886	6.65	57	1.10	0.576	0.104	0.051
1981	199,500	78,600	12	7	155	0.78	3	0.04	705	3.53	39	0.50	0.592	0.099	0.037
1982	329,700	209,900	33	13	179	0.54	0	0.00	1,387	4.21	65	0.31	0.239	0.084	0.000
1983	436,700	98,000	63	91	239	0.55	7	0.07	2,868	6.57	293	2.99	0.218	0.057	0.017
1984	617,100	312,300	78	100	244	0.40	0	0.00	3,620	5.87	275	0.88	0.413	0.039	0.000
1985	580,900	255,000	82	100	534	0.92	0	0.00	1,477	2.54	343	1.35	0.490	0.167	0.000
1986	589,200	276,100	88	100	749	1.27	0	0.00	1,993	3.38	93	0.34	0.605	0.157	0.000
1987	539,200	205,800	85	100	716	1.33	1	0.00	2,005	3.72	58	0.28	0.480	0.167	0.010
1988	687,000	395,300	87	100	867	1.26	1	0.00	2,520	3.67	226	0.57	0.336	0.182	0.003
1989	416,600	217,700	84	100	430	1.03	1	0.00	1,085	2.60	168	0.77	0.428	0.189	0.003
1990	429,100	475,900	96	100	176	0.41	0	0.00	1,174	2.74	353	0.74	0.585	0.070	0.000
Mean			61	58		0.97		0.03		4.89		1.40		0.113	0.012

$$R_2 = N_0 * (1 - \Psi) * \exp^{-(M_2 + F)} \qquad (2)$$

Both equations contain N_0 and thus can be simplified to the expression

$$\Psi = \frac{\Phi}{(\Phi + 1)}, \qquad (3)$$

where

$$\Phi = \frac{R_1 \exp^{-(M_2 + F)}}{R_2 \exp^{-M_1}}. \qquad (4)$$

This formulation assumes that all individuals mature as either 1SW or 2SW fish. This is reasonable because returns of 3SW and older fish have been insignificant during the study period (typically less than 1% of the total runs).

The 1SW:2SW ratio has frequently been used as an index of 1SW maturation rate. However, sea-age classes are often affected by different patterns of marine mortality, particularly fishing mortality. Thus, the 1SW:2SW ratio is a satisfactory measure of maturation rate in only those instances where fishing mortality is constant over time and in fact is linearly related to 1SW maturation rate under these conditions. We know of considerable contrast in the fishing mortality time series for North American 2SW stocks, thus Ψ must be calculated.

Smolt size and age

The size of smolts as a factor affecting return rate and sea-age of maturation could not be directly evaluated in this study because smolt sizes were not available. However, comparability of the smolt releases in the two river systems and the transition from smolt releases of predominantly two-year-old fish to releases of yearling smolts raised concerns about the role smolt size may have had on the observed pattern of return rate and maturation. To address this concern, for each scale the length (mm) of the freshwater zone (taken as the distance from the focus to the end of the freshwater zone along the 360° axis of the scale) was measured (Fig. 2). Back-calculated lengths were not computed because of incomplete data on length at recapture; therefore, freshwater zone lengths were interpreted as an indication of smolt size. The analysis of freshwater zone lengths and other scale measurements were restricted to 2SW salmon owing to the extremely low returns of 1SW salmon to the Connecticut River (Table 1). Cleaned and mounted scales were measured with an Optimas image processing system. Sample sizes are provided in Table 2.

Statistical analysis of freshwater zone lengths was complicated by the lack of a consistent pattern for which stock had the greater zone-length mean. Freshwater zone lengths were compared among years and between stocks with a two-way analysis of variance

(ANOVA). However, the results of this ANOVA are not reported because the interaction term was significant. Instead, a one-way analysis of variance, with stock as the factor, was conducted for each smolt year.

Circuli spacing patterns and post-smolt growth

The spacing of scale circuli deposited during the first year at sea was measured from scales of 2SW salmon returning to the Penobscot and Connecticut rivers. The first spacing was measured between the first circulus of the post-smolt growth zone and the next circulus, and all successive pairs were measured until the end of the post-smolt growth zone. The end of the zone was recognized when circuli spacings began to widen a second time, indicating the beginning of the second sea summer (Fig. 2). All measurements were made along the 360° axis of the scale.

Growth during the post-smolt period was evaluated from the circuli spacings in three regions of the scale. We used the spacing patterns as growth indices because, in salmonids and other fish, scale intercirculi spacing is directly related to growth (Doyle et al., 1987; Barber and Walker, 1988; Fisher and Pearcy, 1990). Three regions of the scale were selected to correspond with seasons of the calendar year. The circuli pair spacings used to represent the "spring" period, or first entry of salmon into the marine environment, was fixed to pairs "two" through "six" (Fig. 3). The "summer" period, or the period of maximum growth, was represented by the five widest and contiguous mean spacings. The first sea "winter" period was represented by the five narrowest and contiguous mean spacings. The general assumption that regions of the scale are associated with seasons of the year is supported by the analysis of post-smolt scales from tagged fish and ocean recaptures (Friedland et al., 1993). The three growth zones were identified from the patterns of mean spacings of circuli pairs from all the data for a smolt year cohort and sea-age. This approach was used because it was not possible to identify seasonal growth zones in the spacing patterns for all individuals because of the variability of these patterns.

Cumulative growth during the post-smolt period was represented by the number of circuli in the post-smolt growth zone and the length of the zone itself. A circuli count was determined for each cohort and sea-age group. The count was based on the mean circuli spacing patterns also used to identify growth
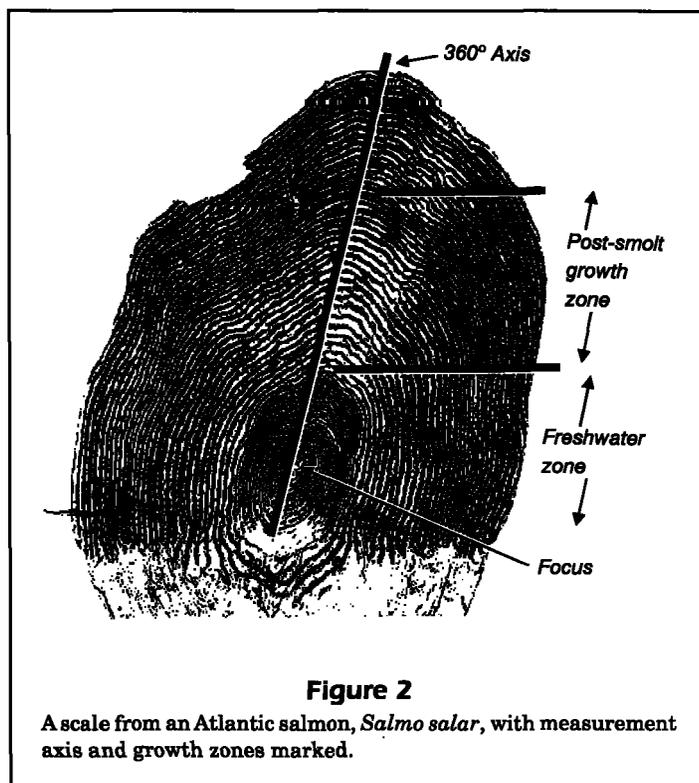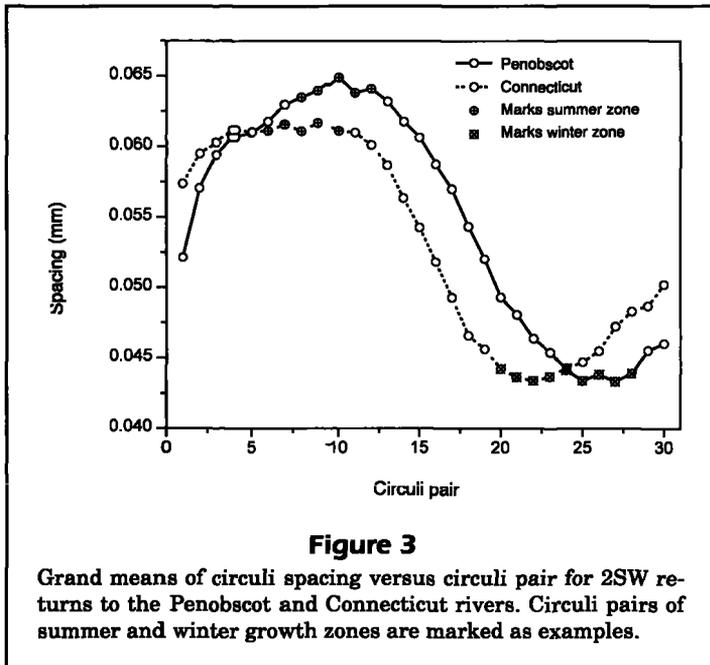

Figure 2

A scale from an Atlantic salmon, *Salmo salar*, with measurement axis and growth zones marked.

Table 2

Sample sizes and post-smolt growth-zone circuli counts for 2SW Atlantic salmon returns to the Penobscot (Pen) and Connecticut (Conn) Rivers.

Smolt year	Sample size		Circuli count	
	Pen	Conn	Pen	Conn
1977	75	25	26	22
1978	65	77	20	24
1979	75	168	24	21
1980	65	24	24	24
1981	75	9	26	17
1982	75	52	26	20
1983	75	81	27	20
1984	40	45	25	21
1985	108	186	28	22
1986	74	70	27	22
1987	51	75	23	24
1988	64	170	26	23
1989	83	121	26	23
1990	95	179	26	22
Mean			25	22

zones. The count consisted of the number of circuli from the end of the freshwater zone to the first circulus of the third winter circuli pair. The post-smolt

Figure 3

Grand means of circuli spacing versus circuli pair for 2SW returns to the Penobscot and Connecticut rivers. Circuli pairs of summer and winter growth zones are marked as examples.

growth zone length was taken as the distance from the last circulus in the freshwater zone to the outer circulus of the third circuli pair of the winter zone measured along the 360° axis of the scale (Fig. 2). This distance reflects the average spacing of circuli and the number of circuli deposited during the post-smolt period.

Comparison of post-smolt growth

Circuli spacing patterns and lengths of the post-smolt growth zone for both the Penobscot and Connecticut stocks were compared by analysis of variance. Circuli spacings for the spring, summer, and winter zones were compared by means of two-way analysis of variance with year and stock as factors. The growth zone of an individual fish was represented by the mean circuli spacing of the growth-zone circuli pairs identified in the pattern of mean spacings for all fish of that smolt year and stock. In all cases, the interaction terms for these ANOVA's were significant and thus the two-way ANOVA results are not reported. Instead, circuli spacings of both stocks were compared with one-way analysis of variance for each smolt year. The length of the post-smolt growth zone for both stocks was also compared for each year with a series of one-way ANOVA's.

The annual variation in circuli spacing growth-zone indices was compared by using Pearson product-moment correlation. The correlation coefficients were computed by using the seasonal growth-index means for the two stocks.

Results

Return rate and cohort age at maturity

Return rates for both 1SW and 2SW salmon were higher in the Penobscot River than in the Connecticut River. The return rate for 1SW salmon averaged 0.97‰ and ranged from 0.36 to 2.20‰ for the Penobscot stock, whereas for the Connecticut stock the return rate averaged 0.03‰ and ranged from 0.0 to 0.12‰ (Table 1). For 2SW salmon, the return rate for the Penobscot stock averaged 4.89‰ and ranged from 1.98 to 12.69‰, whereas in the Connecticut the return rate averaged 1.40‰ and ranged from 0.28 to 5.11‰. Return rates were significantly different between stocks in a paired t-test ($P<0.01$ for both 1SW and 2SW rates). Despite the differences in the level of 2SW return rates between the two stocks, the pattern of annual variation in 2SW return rates of the two stocks was highly correlated ($r=0.88$, $P<0.01$). Peaks in return rate that occurred with the 1978 and 1983 smolt classes are seen in both time series (Fig. 4A). The relation between the two time series is seen clearly in the normalized or Z-transformed data (Fig. 4B). The transform is simply the observation minus the time-series mean divided by the time-series standard deviation.
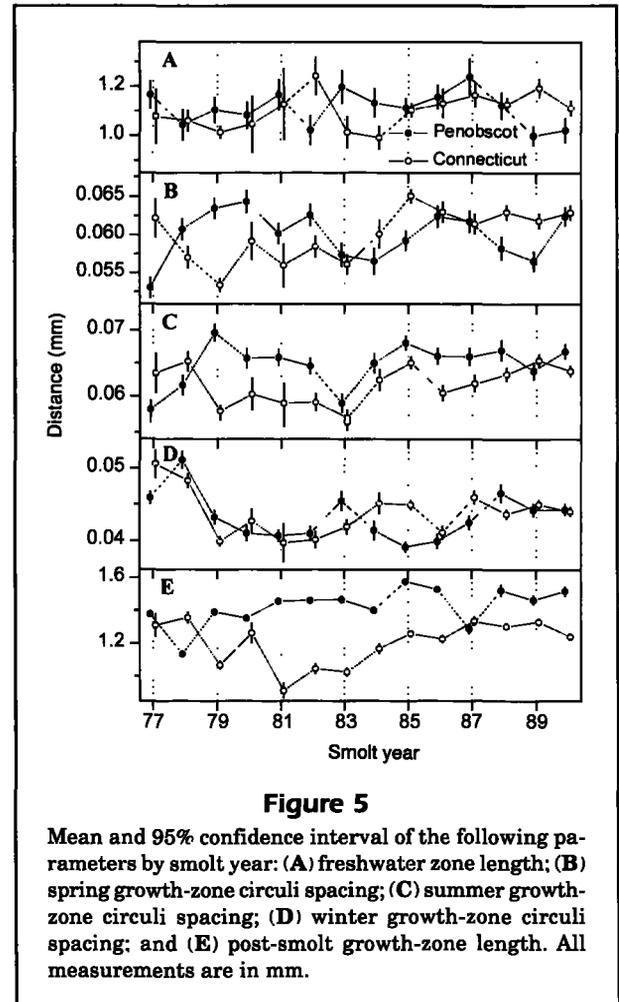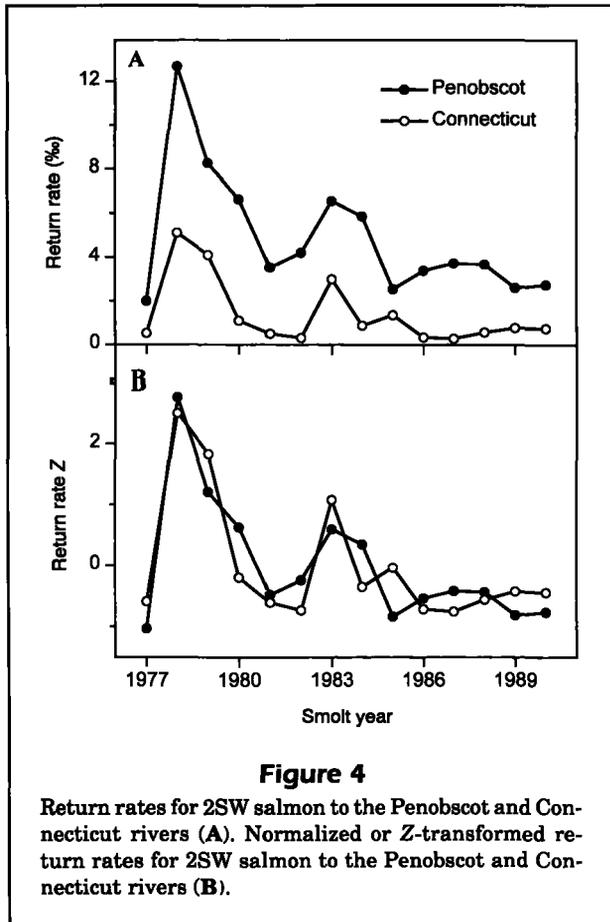
The 1SW fraction for the Penobscot, which averaged 11% during the study period, was an order of magnitude higher than the fraction observed for the Connecticut River (Table 1). The difference between stocks was highly significant (paired t-test, $P<0.01$).

Smolt size and age

Smolt sizes of 2SW returns, as indicated by the lengths of the freshwater zone, showed no systematic differences between stocks. Mean freshwater zone lengths ranged from 1.000 to 1.243 mm for both stocks (Fig. 5A). Significant differences between freshwater zone lengths were found for 6 of the 14 smolt classes, but of those 6 years, there were equal numbers of years with greater means in the Penobscot and Connecticut stocks (Table 3).

Circuli spacing patterns and post-smolt growth

Considerable variation in circuli spacing was evident between stocks and among years. Annual mean circuli spacing indices had an approximate range of 0.04 to 0.070 mm (Fig. 5, B–D). Spring and summer spacing indices averaged greater than 0.060 mm for both

Figure 4

Return rates for 2SW salmon to the Penobscot and Connecticut rivers (A). Normalized or Z-transformed return rates for 2SW salmon to the Penobscot and Connecticut rivers (B).

Figure 5

Mean and 95% confidence interval of the following parameters by smolt year: (A) freshwater zone length; (B) spring growth-zone circuli spacing; (C) summer growth-zone circuli spacing; (D) winter growth-zone circuli spacing; and (E) post-smolt growth-zone length. All measurements are in mm.

the Penobscot and Connecticut stocks, whereas the winter indices averaged less than 0.044 mm. The spring and winter index means were nearly identical for the two stocks, whereas the summer index mean was greater in the Penobscot. The mean number of circuli deposited in the post-smolt growth zone averaged 25 for the Penobscot stock and 22 for the Connecticut stock (Table 2). Post-smolt growth-zone length indices ranged from 0.913 to 1.577 mm and averaged 1.425 mm for the Penobscot stock and 1.204 for the Connecticut stock (Fig. 5E). Differences in the annual seasonal spacing indices and circuli counts were also reflected in the pattern of mean circuli spacings for all years: the Penobscot stock had wider circuli spacing in the summer zone and a greater number of circuli deposited prior to the winter zone (Fig. 3).

Comparison of post-smolt growth

The analyses of variance suggest that post-smolt growth was greater in the Penobscot stock, especially during the summer season. Spring growth indices

ranged from 0.053 to 0.065 mm for both Penobscot and Connecticut origin fish (Fig. 5B). Significant differences between Penobscot and Connecticut spring growth-zone means were found for 10 of the 14 smolt classes, and of those 10 years there were equal numbers of years with greater means for the Penobscot and Connecticut stocks (Table 3). Summer growth indices ranged from 0.057 to 0.069 mm for both Penobscot and Connecticut origin fish (Fig. 5C). Significant differences between Penobscot and Connecticut summer-growth-zone means were found for 11 smolt classes, and of those 11 years, 9 were years in which the Penobscot stock had the greater mean (Table 3). Winter growth indices ranged from 0.039 to 0.051 mm for fish of both Penobscot and Connecticut origin (Fig. 5D). Significant differences between Penobscot and Connecticut winter growth-zone means were found for only for 8 of the 14 smolt classes, and of those 8 years, there were equal numbers of years with greater means for Penobscot and Connecticut stocks (Table 3).

Table 3

Probability of one-way ANOVA for stock effect on freshwater zone length (FW zone), seasonal circuli spacing growth indices, and post-smolt growth zone (PS zone). Bolding indicates significance at $P<0.05$. Pen = Penobscot stock; Conn = Connecticut stock.

| Smolt year | FW zone | Circuli spacing | | | PS zone |
		Spring	Summer	Winter	
1977	0.131	**0.000**	**0.005**	**0.000**	**0.003**
1978	0.659	**0.009**	**0.011**	**0.049**	**0.000**
1979	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
1980	0.529	**0.002**	**0.000**	0.152	**0.000**
1981	0.703	**0.039**	**0.000**	0.487	**0.000**
1982	**0.000**	**0.001**	**0.000**	0.366	**0.000**
1983	**0.000**	0.339	0.066	**0.002**	**0.000**
1984	**0.001**	**0.033**	0.068	**0.004**	**0.000**
1985	0.689	**0.000**	**0.001**	**0.000**	**0.000**
1986	0.473	0.594	**0.000**	0.097	**0.000**
1987	0.081	0.805	**0.002**	**0.000**	**0.010**
1988	0.851	**0.000**	**0.005**	**0.008**	**0.000**
1989	**0.000**	**0.000**	0.149	0.329	**0.000**
1990	**0.001**	0.657	**0.002**	0.758	**0.000**

Years with significant differences

Pen>Conn	3	5	9	4	12
Conn>Pen	3	5	2	4	2

Table 4

Correlation coefficients (r) between Penobscot and Connecticut river circuli spacing seasonal growth indices. Bolding indicates significance at $P<0.05$, $n=14$.

Seasonal growth index	r	P-level
Spring	−0.263	0.364
Summer	−0.018	0.950
Winter	**0.535**	**0.049**

Cumulative growth during the post-smolt year appeared greater in the Penobscot stock. The post-smolt growth zone circuli counts were significantly higher in the Penobscot stock ($P<0.01$). Post-smolt growth zone lengths ranged from 0.913 to 1.577 mm for both Penobscot and Connecticut origin fish (Fig. 5E). Significant differences between Penobscot and Connecticut spring growth-zone means were found for all 14 smolt years, and of these, 12 were years in which the Penobscot stock had a greater mean than the Connecticut stock (Table 3).

Annual variation in circuli spacing was similar for two stocks for one of the three post-smolt growth zones. The correlation coefficient for winter spacing indices was significant, whereas the correlation coefficient for spring and summer indices was not significant (Table 4).

Discussion

The Penobscot and Connecticut stocks exhibited similar interannual patterns of 2SW survivorship despite significant differences between the two stocks in magnitude of survival rate and maturation fraction. Therefore, the sets of conditions affecting the two

stocks during the post-smolt year must to some degree intersect to account for the similarity in the survival-rate time series. At the same time, however, there must also be significant differences in these condition sets to account for the significantly lower survival and maturation fraction found for the Connecticut stock. We have found it instructive to consider those factors that appear to be similar and those that appear to be different for the two stocks.

The scales from Penobscot and Connecticut fish returns had similar freshwater zone lengths, circuli spacing indices in the spring and winter, and a correlated pattern of annual variability between winter growth indices. These similarities should be interpreted in respect to the correlation in annual 2SW survivorship. The survivorship of North American multiseawinter stocks has been related to ocean conditions in the Labrador Sea during winter (Friedland et al., 1993). It has been hypothesized that stocks emanating from various rivers in North America intermix and are acted upon by a common set of survival conditions during the winter season. The coherence of the survival time series for the Penobscot and Connecticut stocks, as well as for other North American stocks, is considered evidence that stocks converge on the same overwintering ground. Scale analysis shows that annual variation in growth indices during winter were correlated, which would be consistent with the assertion that these fish were in the same location during that season. The lack of correlation between spring and summer indices suggests that the fish from the respective stocks were acted upon by differing conditions, possibly while they resided in different areas. These data suggest that fish from the Penobscot River are not fully mixed with fish from the Connecticut River until the winter season, thus supporting the survival hypothesis for all North American stocks in general.

Though smolt sizes, as inferred by the freshwater zone lengths of the scales, were similar for the two stocks, we can not conclusively eliminate freshwater effects from contributing to observed differences in survival. There is a large body of evidence that

illustrates the influence of smolt-size and condition and stocking circumstances on the return rates and yields of salmon stocks (Ward et al., 1989; Hvidsten and Johnsen, 1993; Farmer, 1994; Lundqvist et al., 1994). We lack smolt size information on the fish that did not survive; they may have had a different freshwater zone length-size frequency than that observed for the survivors. Smolt age composition was similar each year and appears unrelated to the differences between stocks. However, the trend in smolt age composition is not similar to the time-series trends in survival and maturity for the two stocks and should be considered along with other factors when evaluating long-term changes in stock performance (Friedland et al., 1993).

Summer circuli spacing and post-smolt growth-zone length data suggest that the Penobscot fish grew faster than the Connecticut fish as post-smolts. These differences may have influenced survivorship and maturation. These data suggest that fish from the Connecticut stock grew more slowly during the post-smolt year than did Penobscot fish, matured as 1SW less frequently, and were more vulnerable to mortality. It is generally accepted that larger individuals are less vulnerable to predation (Peterson and Wroblewski, 1984; McGurk, 1986; Anderson, 1988; Miller et al., 1988; Pepin, 1991; L'Abee-Lund et al., 1993). Therefore, smaller, slower-growing Connecticut salmon may be vulnerable to a wider range of potential sources of mortality. For example, under these conditions, we would predict that Connecticut post-smolts would be vulnerable to predators for a longer period of the post-smolt year than would Penobscot post-smolts. Likewise, smaller post-smolts may not effectively compete with other predators for prey or may experience ontogenetic mismatches with prey resources that are also growing or that may be transient in post-smolt habitats (Brodeur, 1991; Healey, 1991; Levings, 1994).

Sea-age at maturation is partly a growth-related phenomenon associated with the seasonal accumulation of lipid stores (Rowe et al., 1991; Thorpe, 1994). In general, maturation at a certain age has been associated with individual growth rate and other causal effects (Alm, 1959; Svedäng, 1991; Thorpe, 1994); however, the effect of sea growth on maturation in salmon has not always been obvious (Power, 1986; Randall et al., 1986; Myers and Hutchings, 1987). Using sea ranching and cage culture experiments with the same genetic stock of salmon, Saunders et al. (1983) reported evidence supporting a hypothesis that first seawinter temperature minima are critical determinants of maturation in salmon. This work was further supported by Herbinger and Newkirk (1987) who described a relationship between 1SW

maturation and favorable (or perhaps minimum) winter growth. However, the specificity of seasonal growth effects can be challenged by other experimental evidence that shows that spring growth can influence 1SW maturation (Thorpe et al., 1990). In an analysis of the Penobscot stock, Friedland and Haas (1996) showed that maturation fraction varies with summer growth rate of the cohort as indicated by circuli spacing indices for 2SW returns. This finding is further supported by our comparison of Penobscot and Connecticut fish which shows that the stock with the greater summer growth had produced a higher percentage of mature 1SW fish.

How an environmentally driven maturation mechanism would optimize age at maturation is not clear. For salmon stocks with complex maturation age structures, early maturing fish (1SW) are predominantly males; egg-producing females more frequently mature at a later age when their egg production is maximized. Therefore, a shift in age at maturity allows a brood class to receive genes from more than one spawning cohort without significant loss of egg production. This plasticity in spawning age ensures that genes move within the population while remaining robust to environmental effects on the deposition of female gametes, which are limiting (Stearns and Crandall, 1984; Stearns, 1992). However, Atlantic salmon exhibit a wide range of maturation age structures (Power, 1981; Saunders, 1981; Saunders and Schom, 1985) suggesting within-population heterozygosity may also be maintained by protracted freshwater residency that allows many brood years to contribute to a smolt run in a given year.

Genetic influences have also been shown to affect stock-specific patterns of age at maturity (Saunders et al., 1983; Thorpe et al., 1983). However, genetic factors are unlikely to explain the differences between the Penobscot and Connecticut stocks because the Connecticut stock is derived predominantly from the Penobscot gene pool (Rideout and Stolte, 1988). When the Connecticut River broodstock was developed, gametes from Canadian and U.S. origin (Penobscot River broodstock) donor stocks were used. However, the crosses with Canadian genetic sources, as demonstrated with tagging, produced virtually no progeny; therefore it can be concluded that the Connecticut broodstock is principally derived from the Penobscot River broodstock.

The systematic differences in growth, survival, and maturation between these two stocks may be related to their post-smolt migrations. When salmon first enter the marine environment, they move by active and passive mechanisms (Jonsson et al., 1993). Because of the differences in the timing of the smolt migration, the starting point of the post-smolt feed-

ing migration, and changes in the ecology of the ocean habitat of salmon, Penobscot and Connecticut smolts are probably exposed to different predator and prey communities during the course of their migrations. These differences would be expected to manifest themselves in growth differences, and as a consequence, in differences in survival and maturation of the two stocks.

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