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PATTERNS OF POST-SMOLT GROWTH AND EARLY MATURATION OF ATLANTIC SALMON (*SALMO SALAR*)

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ABSTRACT

The annual variation in sea age of maturation for a hatchery dependent stock of Atlantic salmon was compared to variation in post-smolt growth as evidenced by circuli spacing patterns. Simple return rates by age and grilsification fraction, the fraction of the cohort that matured as one-seawinter (1SW) salmon, were compared to the seasonal growth patterns reflected in the scales of smolt class survivors returning as 1SW and 2SW spawners. Using image processing techniques, we extracted inter-circuli distances from 2,244 scale samples. Spacing data for the first year at sea were collected and then expressed as seasonal growth indices for the spring period, when post-smolts first enter the ocean: the summer, when growth appears maximal; and winter, when growth appears to be at a minimum. In general, circuli spacings were wider for grilse than for the 2SW returns of the same smolt cohort. The grilsification fraction was significantly and positively correlated with late summer growth, suggesting that growth during this season is pivotal in determining the proportion of a smolt class that matures early.

I. INTRODUCTION

For Atlantic salmon, *Salmo salar*, age at maturity is highly variable and has important consequences on cohort genetics and stock productivity. For example, cross-cohort reproduction by the maturation of precocious parr and grilse may play an important role in maintaining stock heterozygosity (Schaffer, 1974; Caswell *et al.*, 1984; Saunders & Schom, 1985). At the same time, it is also thought that these life history patterns may have a detrimental effect on population growth due to the lower reproductive potential of grilse versus multi-seawinter salmon (Myers, 1986; Randall, 1989). With such a short life-span and limited reproductive opportunities, shifts to younger age of maturity that are caused or exacerbated by fishing may have a detrimental impact on Atlantic salmon populations (Riddell, 1986). Additionally, as Atlantic salmon have become widely used in sea cage aquaculture, early maturation has been found to have a dramatic, negative effect on operational yield (Herbinger & Friars, 1992). As a result, considerable interest has been placed on determining what factors influence early maturation.

The age at which a salmon matures is influenced by heritable traits and environment. The link between genetics and early maturation has been demonstrated by a range of experimental evidence (Naevdal, 1983; Gjerde, 1984; Ritter *et al.*, 1986; Chadwick *et al.*, 1987). Simply stated, there is a tendency for higher numbers of grilse offspring from grilse parents and multi-seawinter (MSW) offspring from MSW parents (Piggins, 1974; Ritter *et al.*, 1986). There is evidence that environment can also play a crucial role: results from experiments (Saunders *et al.*, 1983; Adams & Thorpe, 1989) and field studies (Martin & Mitchell, 1985; Herbinger & Newkirk, 1987; Scarnecchia *et al.*, 1989) suggest that ocean climate during the post-smolt year influences maturation. In addition, the freshwater environment can influence maturation of both precocious parr and grilse (Hutton, 1937; Saunders, 1981; Scarnecchia, 1983; Rowe & Thorpe, 1990; Jonsson *et al.*, 1991). While previous studies illustrate the role of genotype and environmental factors in maturation, we still lack a mechanistic framework explaining how seasonal growth in both grilse and MSW salmon combine to produce annual patterns of maturation.

Our goal was to reconstruct the post-smolt growth history for a salmon stock with known annual variation in age at maturity. It is assumed that if growth and observed maturation are independent, mechanisms such as smolt age and size, genetics, or unknown factors play a more significant role than post-smolt growth in triggering maturation. Alternatively, a relationship between post-smolt growth and maturation will potentially indicate how post-smolt growth patterns influence age at maturation.

II. MATERIALS AND METHODS

GRILSIFICATION FRACTION

The fraction of a cohort or smolt year class that matures after only a single winter at sea, the grilsification fraction, is usually measured indirectly by the analysis of adult fish returns. The index stock used in this study is the hatchery component of the salmon run in the Penobscot River, Maine, USA. Release groups ranging from 100,000 to 687,000 smolts per year during the period 1973 to 1990 were included in the analysis (Table I). During this period, the hatchery program was in transition; early in the time series releases were mostly two year old smolts, whereas in recent years,

releases were mostly one yearling smolts. Returns of grilse or 2SW salmon to freshwater were enumerated from recreational landings and trap counts from the first fishway trap in the Penobscot River. It is well known that North American salmon stocks have been exploited in commercial fisheries in Canada and Greenland. To account for this, we applied extant exploitation rates for North American stock components maturing as 2SW salmon from recent analyses of fishing mortality and stock abundance (Rago *et al.*, 1993).

The observed return of grilse to freshwater (R_1), given in Equation 1, is the product of the maturation fraction (ψ) and the size of the cohort immediately before grilse return to homewaters and one-seawinter (1SW) fisheries commenced (N_0). Natural mortality of this fraction of the cohort (M_1) is assumed to be zero.

$$(1) \quad R_1 = N_0 \cdot \psi \cdot \exp^{-M_1}$$

The observed return of 2SW salmon (R_2), given in Equation 2, is assumed to be remainder of the cohort that did not mature, and then survives the natural mortality effects for an additional 10 months at sea plus the mortality associated with fishing ($M_2=0.1$ is from Doubleday *et al.*, 1979 and F is given in Table I). The additional time 2SW salmon stay at sea is assumed to be 10 months since 2SW salmon return to the river earlier than grilse.

$$(2) \quad R_2 = N_0 \cdot (1 - \psi) \cdot \exp^{-(M_2 \cdot F)}$$

Both equations contain N_0 and can be simplified to the expression in Equation 3.

$$(3) \quad \psi = \frac{\phi}{(\phi + 1)}$$

where ϕ is equal to the quantity in Equation 4.

$$(4) \quad \phi = \frac{R_1 \cdot \exp^{-(M_2 \cdot F)}}{R_2 \cdot \exp^{-M_1}}$$

This formulation omits the three-seawinter life history pattern which seems reasonable since returns of this age group have been very low during the study period (typically less than 1% of the total run).

Investigators have often used grilse to salmon ratios (the ratio of grilse to 2SW returns) to study maturation in salmon populations. In most instances in both North America and Europe, sea-age classes are affected by different patterns of marine mortality, particularly in the fishing mortality component. The grilse to salmon ratio is satisfactory in instances where fishing mortality is constant over time, and in fact is linearly related to maturation fraction under these conditions.

CIRCULI SPACING PATTERNS AND POST-SMOLT GROWTH

The spacing of scale circuli deposited during the first year at sea was measured for grilse and 2SW salmon returns to the Penobscot River, Maine. Sample sizes are given by sea-age at return and by smolt year (Table II). Scales were cleaned and mounted between glass slides before measurement. Spacing measurements were made with a Bioscan Optimas image processing system (reference to tradename does not suggest endorsement). The first spacing measurement (mm) is formed by the first circulus of the marine zone and the next circulus, and continues with successive pairs until the spacings begin to widen, indicating the beginning of the second sea summer zone. All measurements were made along the 360° axis of the scale (Figure 1).

Circuli spacings record the seasonal events of the first year at sea. Circuli spacing is widest in the region of circuli pairs eight to 14, the post-smolt summer, and narrowest in the region of pairs 20 to 28, the post-smolt winter, for both sea-age groups (Figure 2). Post-smolt scales from tagged fish and ocean recaptures suggest approximate dates of deposition for regions of the scale and specific circuli pairs (Friedland *et al.*, 1993). Circuli pairs seven to 12 had mean deposition dates of July 26 to August 21, indicative of the summer period of maximum growth. Circuli pairs 15, 18, and 19 had mean deposition dates of September 21, 29, and October 9, during autumn. The winter minimum zone, centered on circuli pair 25, was estimated to be deposited in December or January considering the deposition dates for autumn circuli.

From this information, three descriptive indices were determined from the circuli spacing data. Index means of circuli spacing were intended to generally represent three seasons or growth regimes during the post-smolt year. It was not possible to identify seasonal growth zones in the spacing patterns for all individual fish or scales because of the variability of these patterns among individuals. Instead, the zones were identified and computed from the pattern of mean circuli spacings for each age group by smolt year. The zone representing "spring", or first entry into the marine environment, was computed from means for circuli pairs two through six. The zone representing "summer", or the period of maximum growth, included the widest mean spacing and four neighboring mean spacings. The zone representing the first sea "winter" consisted of the minimum mean spacing and four neighboring spacings.

We used the spacing patterns as growth indices, since in salmonids and other fish, scale intercirculi spacing is directly related to growth (Doyle *et al.*, 1987; Barber & Walker, 1988; Fisher & Percy, 1990). We measured mean intercirculi spacings of the three zones as indices of seasonal growth. Thus, narrow spacings indicate slow growth and wide spacings indicate fast growth.

SMOLT AGE AND THE FRESHWATER ZONE LENGTH AS A PROXY FOR SMOLT SIZE

The size of smolts as a factor affecting maturation sea-age was not evaluated in this study because these measurements were not available. However, the transition from predominantly two-year-old to one-year-old smolt releases raised concerns about the role smolt size may have had on the observed pattern of maturation. To address this concern, 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 for each scale. These lengths were interpreted as an indication of smolt size. Backcalculated lengths were not computed because of incomplete data on length at recapture. The

age of smolts was considered by simply evaluating the age composition of the smolt class in respect to the grilsification fraction.

RELATIONSHIP BETWEEN GRILSIFICATION FRACTION AND POST-SMOLT GROWTH

The relationship between grilsification fraction and growth was investigated with correlation analysis. A Pearson correlation compared the circuli spacing indices with the return rate by age and grilsification fraction. The sensitivity of these correlations was explored by using spacing indices formed with higher and lower numbers of circuli pairs in the calculation and by shifting the central circuli pair to the right and left (i.e. earlier or later in the post-smolt year, respectively). For example, we computed additional summer indices using three, seven, and nine circuli pairs, and shifted the zone by as many as 10 pairs to the right and five pairs to left of the center circuli pair criteria (i.e. the widest circuli pair).

III. RESULTS

GRILSIFICATION FRACTION

Grilsification fraction ranged from 0.02 to 0.19 of the cohort for the 1973 to 1990 smolt classes and has shown trends or distinct periods of high or low grilsification rate (Table I). During the late 1970's and again during late 1980's, the fraction increased to 10 to 13% and to 16 to 19%, respectively. During the earlier portions of these decades, the maturation fraction was less than 10% annually.

CIRCULI SPACING PATTERNS AND POST-SMOLT GROWTH

Circuli spacing indices show considerable annual variation and systematic differences between sea-age groups. Circuli spacing indices have an approximate range of 0.04 to 0.07 mm (Table II). Spring and summer spacing indices averaged 0.0598 to 0.0652 mm, whereas the winter indices averaged 0.0434 to 0.0461 mm. The index based on differences between age groups (1SW index minus 2SW index by cohort) was generally positive indicating the grilse spacing indices were larger than their 2SW counterparts within a cohort (Figure 3).

Following the assumption that growth is related to width of the circuli pairs, the data show that spring-summer growth is greater than winter growth, and additionally indicate that grilse grow faster than those members of the cohort destined to return as 2SW salmon. This difference in growth was consistently greater during the winter period. However, comparative growth of grilse and 2SW fish as indicated by circuli spacing was problematic. Comparison of overall spacing pattern was attempted with MANOVA models, but these models were not deemed appropriate because there is no special significance of individual circuli pairs (e.g. circuli deposition is not synchronous among individuals in a smolt class). Typical of the problems encountered in interpreting these tests was a MANOVA run from the 1990 smolt class. The MANOVA compared age groups and used the vectors of all 30 circuli pair spacings as dependent variables. This comparison was found to be insignificant ($p=0.289$, 30 and 100 degrees of freedom) indicating there was no difference between age groups. However, univariate tests indicated significant differences for circuli pairs 19 through 23, the approximate location of the winter growth zone. Thus, the more productive comparisons by

age group can be made based on groups of circuli (i.e. growth indices), because they are selected by comparable features on the scale and do not result in the comparison of individual, unrelated circuli spacings. Comparison of growth indices by age group was in part achieved by performing sign tests on the pattern of growth zone differences depicted in Figure 3. These tests indicate spring and summer indices were not significantly different ($p=0.814$ and $p=0.239$, respectively), whereas the winter indices were different between ages ($p=0.002$).

SMOLT AGE AND THE FRESHWATER ZONE LENGTH AS A PROXY FOR SMOLT SIZE

Smolt size, as indicated by the length of the freshwater zone, was generally higher for fish that returned as grilse until the mid-1980s (Figure 4). For cohorts in the early part of the time series, when the releases were predominantly two-year-old smolts, the distribution of freshwater zone lengths for 1SW returns were often greater than the distribution of freshwater zone lengths for 2SW returns of the same cohort. In later years of the time series, these length distributions were generally overlapping indicating that grilse and 2SW returns were derived from the same size distribution of smolts. This suggests that smolt size may be a factor affecting age at maturity. However, there has been an increase in the proportion of one-year-old smolts in the releases while the grilsification fraction has increased. In fact, the percentage of yearling smolts was significantly correlated with the grilsification fraction ($r=0.549$, $p=0.018$). This is the opposite situation from what would have been expected if smolt size were the determinant of maturation. Size at smolting appears to predispose some individuals to early maturation. However, the population trends in maturation we have observed in this stock appear more related to smolt age than size.

RELATIONSHIP BETWEEN GRILSIFICATION FRACTION AND POST-SMOLT GROWTH

Two significant correlations emerged from the comparison of seasonal circuli spacing indices with return rates and grilsification fraction. The return rate of grilse and the grilsification fraction were significantly correlated with the summer growth index for 2SW returns (Table III). Both correlations were positive indicating increased summer growth of 2SW fish was related to increased returns of grilse and a higher grilsification fraction.

The sensitivity analysis indicated that indices were relatively robust to the number of circuli pairs included and the center spacing pair used to calculate the index. Correlation coefficients are plotted against relative center spacing position for the nine combinations formed by the three seasonal growth indices and the return rates and grilsification fraction (Figure 5). Locations of circuli pairs for spring or first marine indices were fixed, whereas the centering criteria circuli pairs for summer and winter indices were variable. On average, the summer indices were centered at circuli pairs 9.8 and 11.3 for grilse and 2SW returns, respectively. The average position of the winter indices was centered at circuli pairs 23.4 and 25.1 for grilse and 2SW returns, respectively. Each panel has two sets of coordinates plotted, one for grilse returns and the other for 2SW returns. The cluster of points at each centering location on the abscissa reflects the feasible number of circuli pairs that could be included in the index at that position (i.e. indices computed from three, five, seven, or nine circuli pairs). The results generally confirm observations in Table III with one important exception. The significant correlation observed between 2SW summer growth, and grilse return rate and grilsification rate is improved upon when the indices are centered three circuli pairs to the right or later in the post-smolt year. Using the mean date of circuli deposition observed for

tagged and experimentally caught fish, it would indicate that grilsification fraction is most influenced by growth in 2SW salmon occurring in late August and early September.

IV. DISCUSSION

The main finding of this study is the positive correlation between the growth of 2SW salmon during late summer and the fraction of the cohort that matures as grilse. This is a surprising result considering maturation is related to growth (Alm, 1959). It would have been expected that growth in grilse would be related to the grilsification fraction. However, we have come to the conclusion that it is important to consider growth patterns of the entire cohort while it divides into maturing and non-maturing components.

Consider the hypothetical distribution of summer growth rates for two cohorts or year classes, one cohort with a low grilsification fraction and another with a high grilsification fraction (Figure 6). When we measured the distribution of summer growth rates for a cohort, we actually measured growth rates for the two sub-components of the cohort, rates observed for grilse returns and rates observed for 2SW returns. In Figure 6, these groups are represented by counts to the right of the vertical bar (the bar is an assumed growth rate threshold associated with maturation) for grilse returns, and to the left for 2SW returns. During the high grilsification year, a larger proportion of the cohort has growth that surpasses this threshold than during the low grilsification year. If these two hypothetical years are contrasted, the mean growth rates for 2SW returns will have a larger absolute difference than the means for grilse returns. When considering a time series of years having a range of grilsification fractions, the distribution of mean growth rates of 2SW salmon would be expected to have a higher variance than the distribution of means for grilse. Therefore, our results suggest the grilsification fraction is correlated with the mean location of the distribution of 2SW growth rates since this distribution is assumed to reflect the fraction of the cohort that exceeds the growth threshold for maturation. We believe the annual pattern of growth rates for grilse returns fails to correlate with grilsification fraction because of the low variance of the annual means. This argument is support by the correlation between summer growth in 2SW fish and grilsification fraction and by the generally higher coefficients of variation associated with 2SW growth indices (Table II), which is taken to reflect greater variability in growth. However, the hypothesis is not supported by the insignificant differences in summer growth of grilse and 2SW fish. In only 11 of 18 years did grilse growth exceed 2SW growth, and it was much lower for the 1985-87 cohorts which were high grilsification years. Though the summer growth patterns do not support the model, they do not argue against it either, and we would suggest that other factors, such as events during other time of the year and variation in migration patterns, may be determining the maturation of many of the grilse fish.

Our findings do not challenge the view that maturation in salmon populations is controlled by a combination of genetic and environmental factors (Saunders, 1986). However, what our results do accomplish is to provide a mechanistic framework on how annual patterns of grilsification would develop in a wild or hatchery dependent stock. Post-smolts grow rapidly during their first spring and summer at sea, with circuli spacing patterns providing evidence of faster growth for individuals that mature as grilse. It appears that the fraction of the cohort that matures as grilse is a function of growth of the entire cohort. With knowledge of this mechanism, the possibility of developing

predictive models of annual grilsification rate exist. For the Penobscot stock, we suspect growth during late summer is related to grilsification fraction. With additional information of stock distribution, we would know approximately where and when to look for environmental correlates.

Variable age of maturation is frequently viewed as an adaptation used by individual salmon stocks to expand range and exploit marginal habitats. Variation in age of maturation has been found to vary with characteristics of freshwater habitat (L'Abée-Lund, 1991; Jonsson *et al.*, 1991) and is manifested in patterns of stock specific growth and developmental rates (Saunders, 1981; Thorpe *et al.*, 1983). Some stocks have been shown to have different energy allocation strategies related to grilsification patterns (Herbinger & Newkirk, 1990). If predictions concerning the desirability of having cross-cohort reproduction are true, the evolution of growth rate characteristics that return a desired fraction of the cohort annually would be expected. These growth characteristics would have to complement migration requirements and ocean conditions faced by the stock. Therefore, the findings for the Penobscot River stock may be relevant only to this and allied stocks, and the pivotal growth season in deciding grilsification may be earlier or later in the year for another stock. Though not directly tested, analyses by Peterman (1985), Martin & Mitchell (1985), and Thorpe (1994) suggest other times of the year may be critical to deciding grilsification fraction.

The role freshwater growth plays in deciding maturation is not clear. Hutton (1937) proposed the inverse ratio hypothesis stating that older smolts return at a younger sea-age. Evidence both supporting and contradicting this hypothesis have been observed for many stocks (Gardner, 1976; Bailey & Saunders, 1984; Bielak & Power, 1986; Skilbrei, 1989). Recent studies suggest there may be a pre-disposition for grilsification decided by the energy stores accumulated by parr which takes place well before marine growth influences (Rowe & Thorpe, 1990; Thorpe *et al.*, 1990). The results reported here do little to clarify this situation. We observed large grilse returns derived from the same size and age distribution of smolts that produced 2SW returns, yet also saw evidence that larger smolts were predisposed to become grilse. This paradox suggests that smolt size, and thus the effects associated with the freshwater environment, plays only a minor role in deciding population grilsification trends. However, we cannot ignore the relationship between age composition of the smolt class and grilsification fraction. The shift to yearling smolts was achieved with accelerated incubation procedures which were not viewed as genetically selective. The question becomes whether the freshwater growth regime, independent of smolt size, affected the pattern of grilsification. Our data is not structured to test this effect or end the debate.

We have shown that late summer post-smolt growth can serve as an effective indicator of the grilsification fraction. However, this correlation does not explain what factors influence grilsification as grilse. Grilsification of an individual fish represents the cumulative effects of a full year of sea growth and other factors (Alm, 1959; Svedäng, 1991; Thorpe, 1994). The role of sea growth has not always been the most obvious cause of observed patterns of annual grilsification (Power, 1986; Randall *et al.*, 1986; Myers & Hutchings, 1987). Utilizing sea ranching and cage culture experiments with the same genetic stock of salmon, Saunders *et al.* (1983) reported evidence supporting a hypothesis of critical first seawinter temperature minima as a determinant of maturation of salmon. This work was further supported by Herbinger & Newkirk (1987) who described a relationship between grilse maturation and good (or perhaps minimum) winter growth. However, the specificity of seasonal growth effects can be challenged by other experimental evidence which shows spring growth can influence grilsification (Thorpe *et al.*, 1990). Our results suggest a more

complex set of interactions are at work. The late summer post-smolt growth rate appears to influence the fraction of the cohort that matures, but the most consistent difference between grilse and 2SW returns was found in their winter growth rate (Figures 2 and 3). Judging from our own and others' results, it appears that the grilsification mechanism is environmentally plastic. At least for this stock, individuals that experience rapid summer growth are in a physiological position or state to sustain the winter growth necessary to mature.

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Table I. Smolt releases and returns of grilse and 2SW components to the Penobscot River, Maine. Return rates are computed by sea-age based on the release of 1,000 smolts. Fishing mortality is instantaneous annual F for ocean fisheries harvesting US Stocks. Grilsification fraction of pre-fishery cohort that matures as grilse as per formulae in text.

Smolt Year	Smolt Release	Yearling Smolts %	Grilse		2SW		Fishing Mortality	Grilsification Fraction
			Return	Rate %	Return	Rate %		
1973	108,200	11	31	0.29	917	8.48	0.422	0.02
1974	100,200	34	45	0.45	563	5.62	0.486	0.04
1975	110,600	14	75	0.68	581	5.25	0.298	0.08
1976	234,800	23	44	0.19	1,547	6.59	0.473	0.02
1977	338,500	34	123	0.36	671	1.98	0.511	0.09
1978	202,500	30	203	1.00	2,570	12.69	0.356	0.05
1979	296,300	17	652	2.20	2,454	8.28	0.433	0.13
1980	584,600	63	888	1.52	3,886	6.65	0.576	0.10
1981	199,500	12	155	0.78	705	3.53	0.592	0.10
1982	329,700	33	179	0.54	1,387	4.21	0.239	0.08
1983	436,700	63	239	0.55	2,868	6.57	0.218	0.06
1984	617,100	78	244	0.40	3,620	5.87	0.413	0.04
1985	580,900	82	534	0.92	1,477	2.54	0.490	0.17
1986	589,200	88	749	1.27	1,993	3.38	0.605	0.16
1987	539,200	85	716	1.33	2,005	3.72	0.480	0.17
1988	687,000	87	867	1.26	2,520	3.67	0.336	0.18
1989	416,600	84	430	1.03	1,085	2.60	0.428	0.19
1990	429,100	96	176	0.41	1,174	2.74	0.585	0.07
Mean		52		0.84		5.24		0.10

Table II. Sample sizes for scale analysis and mean circuli spacing for spring, summer, and winter growth indices.

Smolt Year	Sample Size		Mean Circuli Spacing (mm)					
	Grilse Returns	2SW Returns	Grilse Returns			2SW Returns		
			Spring	Summer	Winter	Spring	Summer	Winter
1973	17	70	0.0629	0.0653	0.0483	0.0604	0.0633	0.0437
1974	21	75	0.0647	0.0650	0.0515	0.0561	0.0632	0.0421
1975	23	68	0.0654	0.0648	0.0495	0.0566	0.0601	0.0475
1976	23	70	0.0626	0.0671	0.0462	0.0633	0.0640	0.0412
1977	72	75	0.0576	0.0630	0.0487	0.0532	0.0581	0.0459
1978	66	65	0.0593	0.0662	0.0470	0.0608	0.0617	0.0512
1979	52	75	0.0627	0.0680	0.0472	0.0635	0.0696	0.0432
1980	18	65	0.0655	0.0669	0.0433	0.0644	0.0658	0.0410
1981	59	75	0.0597	0.0653	0.0434	0.0602	0.0659	0.0407
1982	65	75	0.0616	0.0661	0.0460	0.0626	0.0646	0.0409
1983	63	75	0.0638	0.0649	0.0464	0.0574	0.0589	0.0454
1984	57	40	0.0645	0.0647	0.0430	0.0565	0.0650	0.0414
1985	64	108	0.0634	0.0633	0.0446	0.0593	0.0681	0.0391
1986	58	74	0.0616	0.0607	0.0414	0.0624	0.0661	0.0400
1987	65	51	0.0609	0.0616	0.0445	0.0618	0.0660	0.0425
1988	70	64	0.0611	0.0674	0.0459	0.0583	0.0670	0.0466
1989	105	83	0.0604	0.0664	0.0454	0.0566	0.0639	0.0442
1990	43	95	0.0594	0.0670	0.0468	0.0625	0.0668	0.0443
Mean	52	72	0.0621	0.0652	0.0461	0.0598	0.0643	0.0434
Standard Deviation			0.0022	0.0020	0.0024	0.0031	0.0030	0.0030
Coefficient of Variation			3.6	3.0	5.3	5.2	4.7	6.9

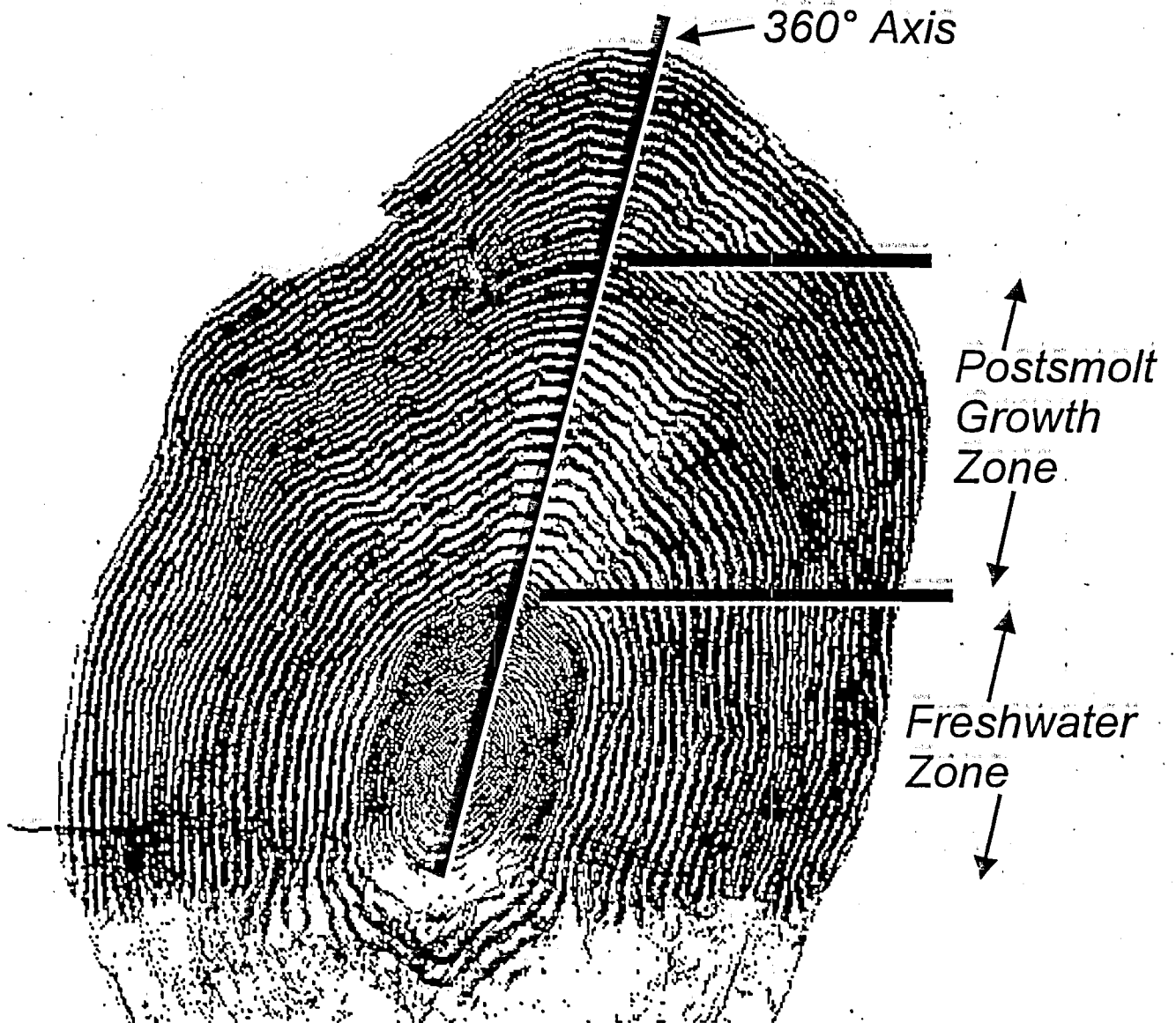
Table III. Matrix of Pearson correlation coefficients between grilse return rate, 2SW return rate, and grilsification fraction (across top), and grilse seasonal growth indices and 2SW seasonal growth indices (left side). N=18 for all correlation coefficients. * marks significant correlations at $p=0.05$.

		Grilse		2SW		Grilsification	
		Return Rate		Return Rate		Fraction	
		r	p-level	r	p-level	r	p-level
Growth of Grilse Returns	Spring	0.04	0.87	0.24	0.34	-0.22	0.37
	Summer	0.09	0.72	0.38	0.13	-0.22	0.37
	Winter	-0.33	0.18	0.22	0.37	-0.42	0.09
Growth of 2SW Returns	Spring	0.41	0.09	0.28	0.27	0.03	0.89
	Summer	0.57	0.01 *	-0.14	0.57	0.47	0.05 *
	Winter	-0.02	0.93	0.44	0.07	-0.15	0.55

LIST OF FIGURES

1. Salmon scale with measurement axis and growth zones marked.
2. Grand means of circuli spacing versus circuli pair for grilse and 2SW returns to the Penobscot River, Maine.
3. Differences (grilse minus 2SW) in seasonal circuli spacing indices by smolt year for returns to the Penobscot River, Maine.
4. Total length of the freshwater zone of scales for grilse and 2SW returns versus smolt year. Box encloses 25 to 75 percentiles, whisker encloses 5 to 95 percentiles.
5. Multi-pane plot of Pearson correlation of grilse return rate, 2SW return rate, and grilsification fraction, versus position of the center circuli used in index calculation for the spring, summer, and winter spacing indices. Filled circles are for grilse returns and open circles are for 2SW returns.
6. Hypothetical depiction of the distribution of summer growth rate for two cohorts, one cohort having a low grilsification fraction and the other having a high grilsification fraction. The vertical bar indicates a threshold amount of growth necessary for an individual to achieve maturation.

Figure 1



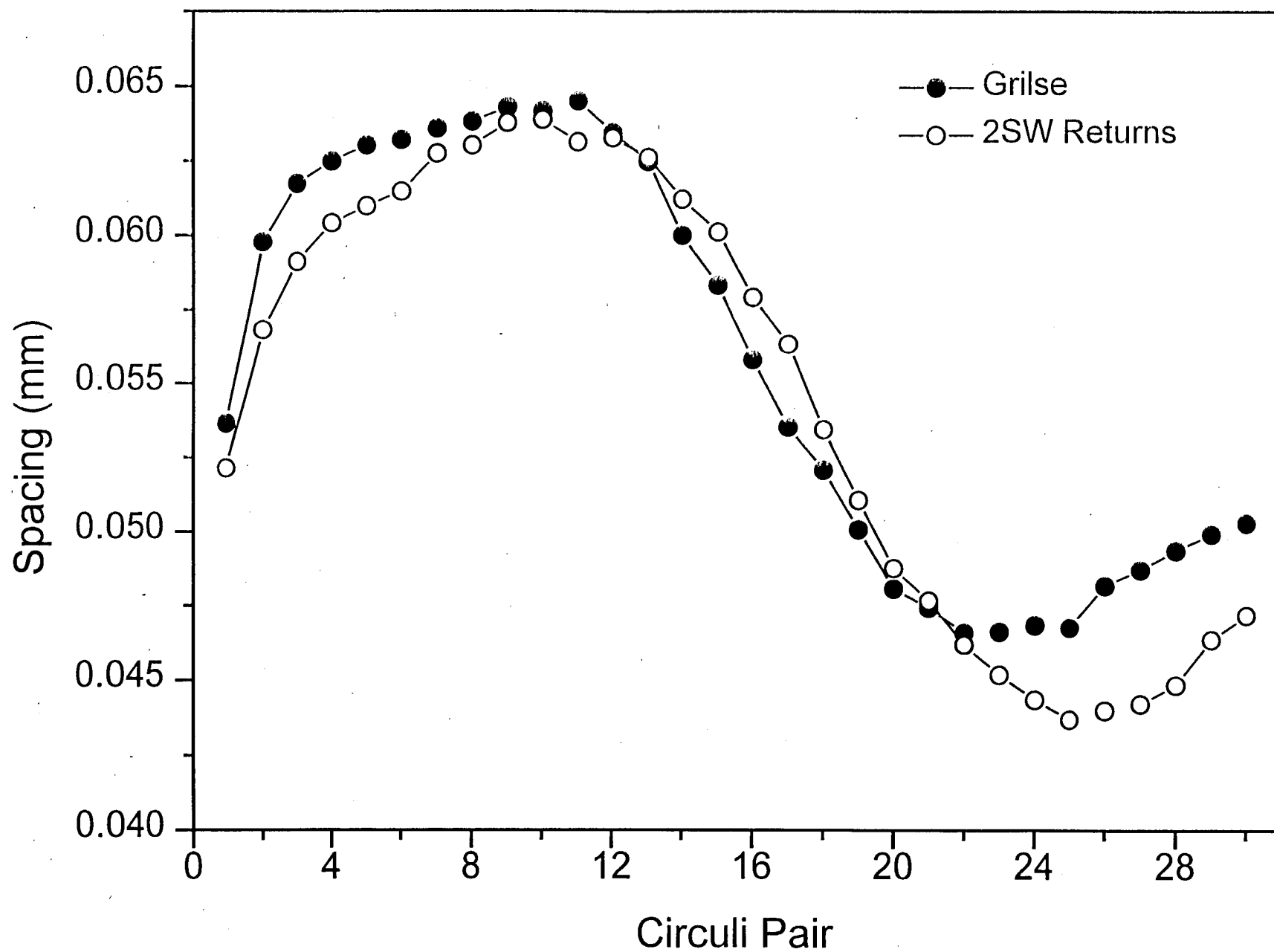


Figure 2.

Figure 3

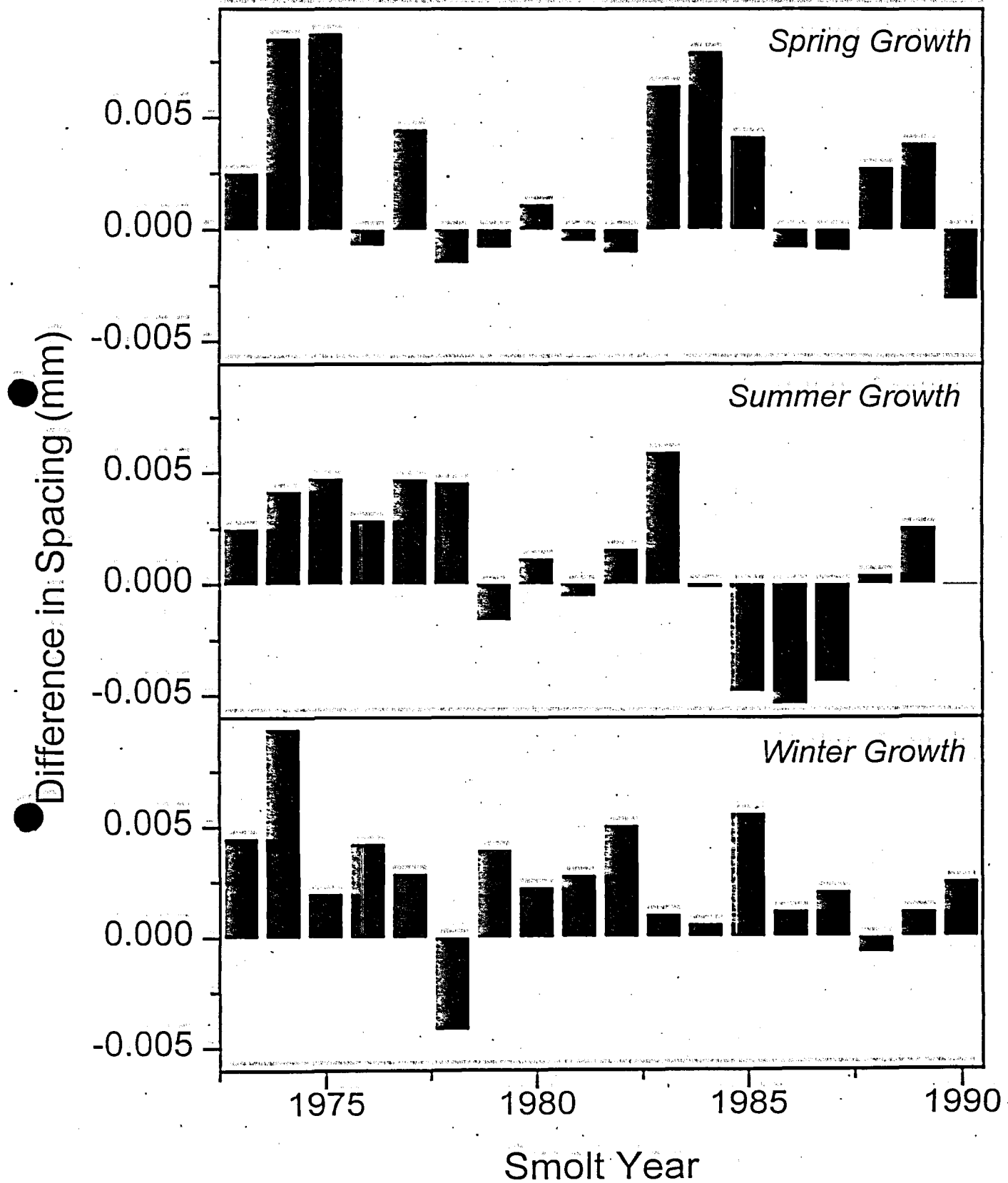
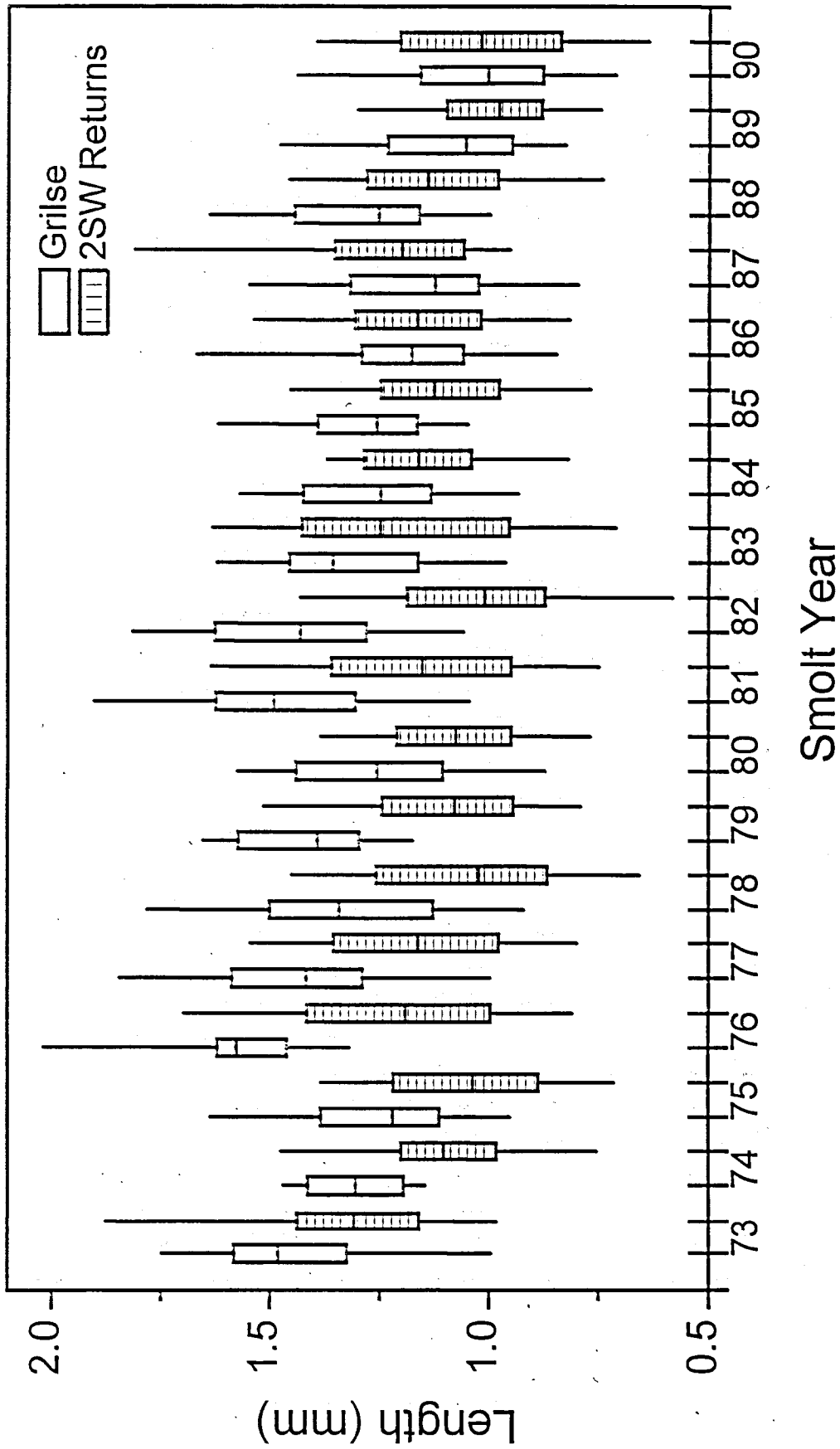


Figure 4



Circuli Spacing Data Extracted from Scales of Grilse(●) and 2SW(○) Returns

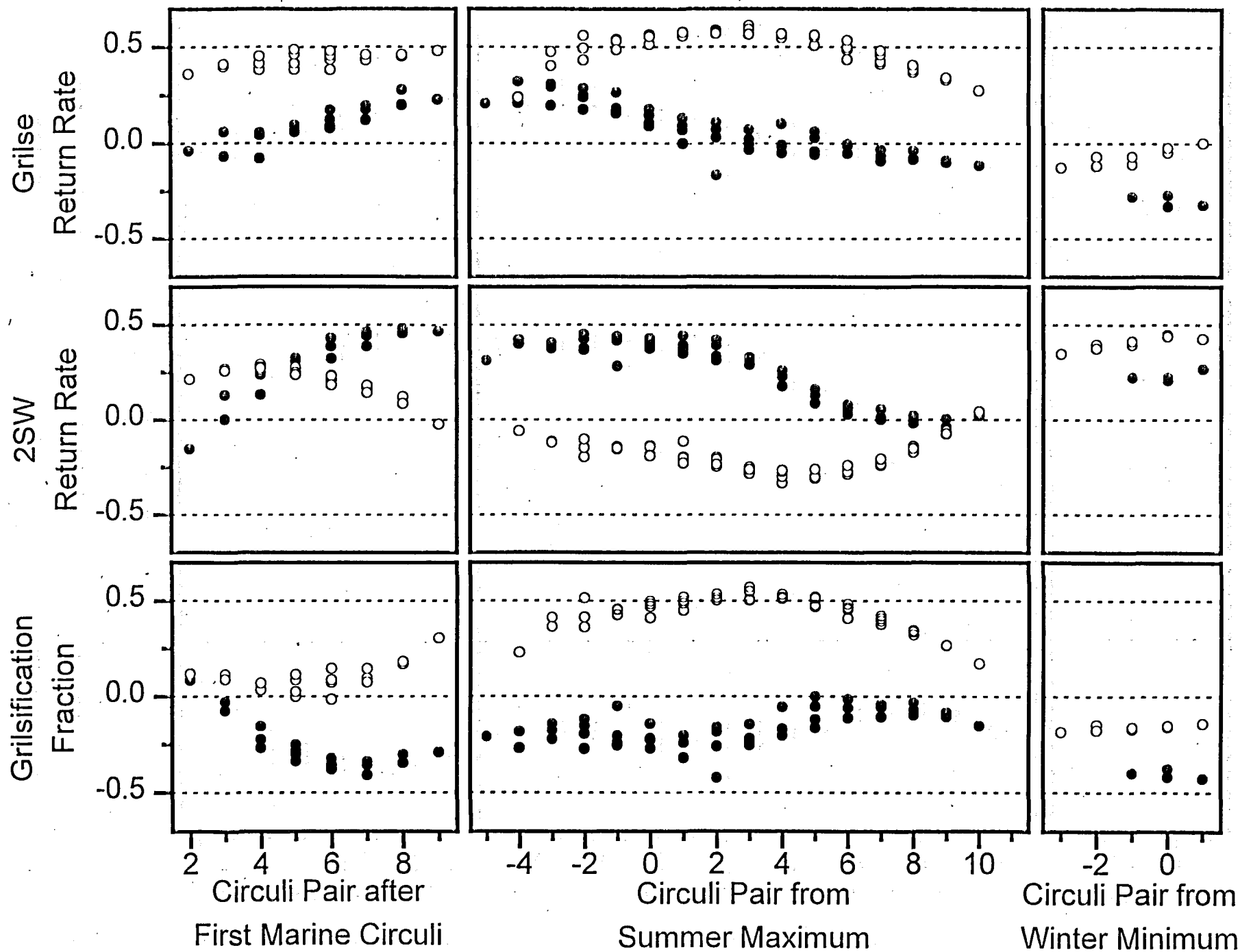


Figure 5

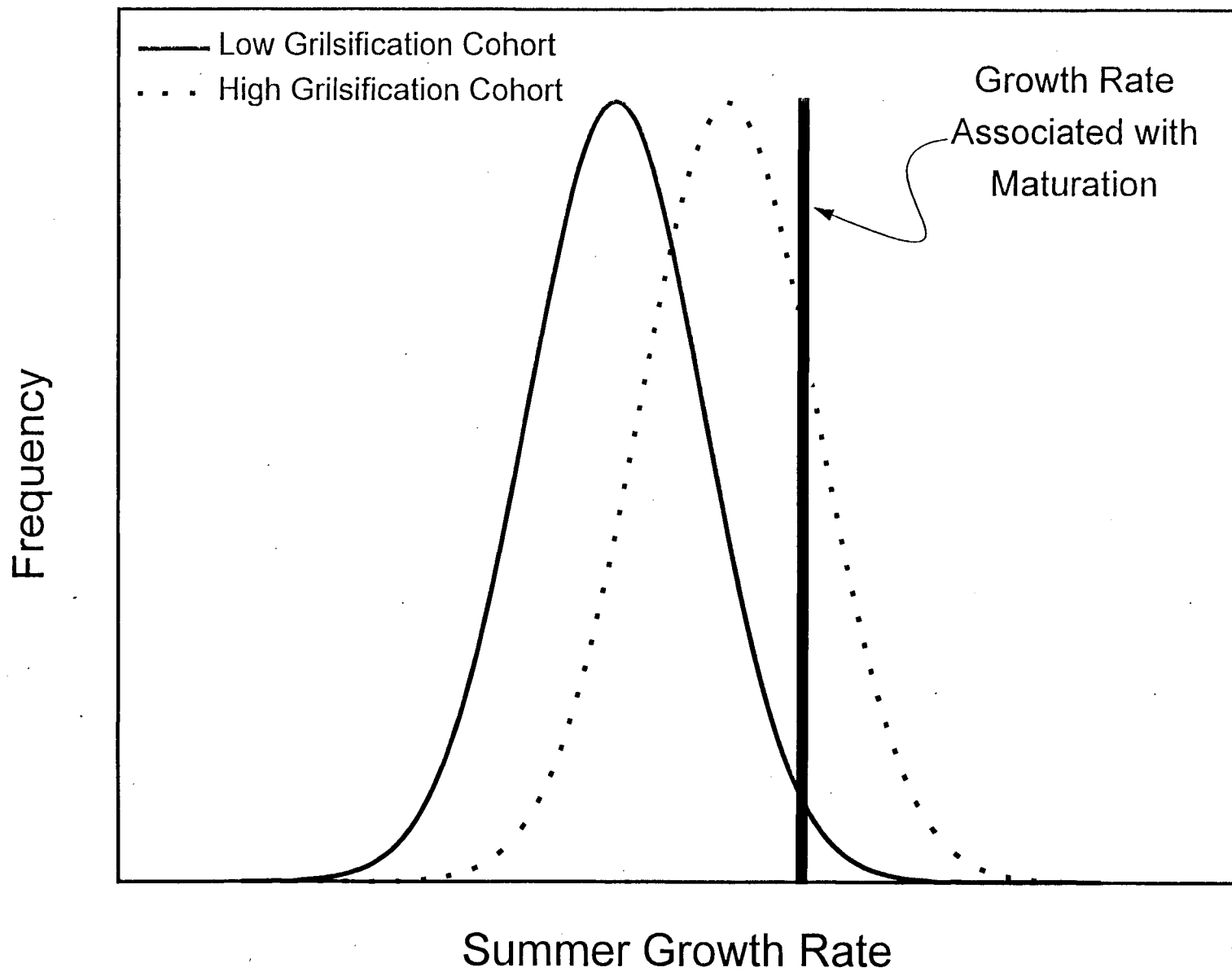


Figure 6.