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Futher evaluation of juvenile Atlantic salmon (*Salmo salar* L.) abundance in the Experimental Ponds Area relative to subsequent adult returns to the Gander River and the empirical evidence for density-dependent marine mortality

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Abstract

A marine survival ratio index was calculated as the number of adult salmon returning to the Gander River divided by the total juvenile salmon populations in the Experimental Ponds Area (EPA) at the headwaters of the river in the previous spring. This survival index increased more than four-fold in the first four years (1992-95) following closure of the commercial fishery in 1992 but then dropped moderately in 1996 and then precipitously in 1997, in concert with rapidly increasing juvenile abundance, a pattern consistent with an interpretation of density-dependent mortality. Juvenile abundance was low in 1998 leading to a prediction of an increase in the marine survival index in 1999; this prediction is confirmed in the present study. We herein extend the relationship between the marine survival index and EPA juvenile abundance further back in time by using long-term records of adult returns to the Salmon Brook fishway as an index of whole river returns. This analysis indicates that the apparent negative density dependence is consistent over a span of slightly more than two decades. The EPA juvenile abundance increased from very low levels in 1998 to near record levels in 1999. If the density-dependent model is correct, marine survival this year should be low and year 2000 returns of small adult salmon to the Gander River should be only 13,782 which is far below the conservation requirement of 21,828. In contrast, small adult returns are predicted to increase to a record level of 49,073 if the high survival index calculated for 1999 is applied to year 2000 returns. Continued monitoring of the adult returns in 2000 should provide a strong test of the apparent historic relationship.

Résumé

Un indice du taux de survie en mer a été calculé sous la forme du rapport entre le nombre de saumons adultes revenant à la rivière Gander et la population totale de saumons juvéniles se trouvant, au printemps précédent, dans la zone des lacs expérimentaux (EPA) située en amont de la rivière. L'indice de survie a plus que quadruplé au cours des quatre premières années (1992-1995) suivant la fermeture de la pêche commerciale en 1992, avant de diminuer de façon modérée en 1996 et abruptement en 1997, dans le contexte d'une augmentation rapide de l'abondance des juvéniles, une tendance conforme à l'interprétation d'une mortalité dépendante de la densité. La faible abondance des juvéniles en 1998 laissait présager une hausse du taux de survie en mer pour 1999, tout comme le confirme la présente étude. Sur ce, nous remontons plus loin dans le temps afin d'étudier la relation entre l'indice du taux de survie en mer et l'abondance des juvéniles dans la zone EPA. Les registres à long terme du nombre d'adultes comptés à la passe migratoire du ruisseau Salmon ont servi d'indice pour les remontées totales dans la rivière. Leur analyse démontre que la dépendance négative manifeste à la densité reste inchangée depuis un peu plus de deux décennies. L'abondance des juvéniles dans la zone EPA, pourtant très faible en 1998, a atteint un niveau presque sans précédent en 1999. Si le modèle de dépendance à la densité est exact, le taux de survie en mer sera faible cette année et seulement 13 782 petits adultes remonteront la rivière Gander en 2000, ce qui est loin de satisfaire aux besoins de conservation de 21 828. Par contraste, en appliquant le taux de survie élevé calculé pour 1999 aux remontées de l'an 2000, on prévoit que le nombre record de 49 073 petits adultes remonteront la rivière. Le maintien de la surveillance des remontées d'adultes en 2000 devrait permettre d'éprouver sérieusement la relation historique apparente.

Introduction

The number of small adult salmon returning to the Gander River should be primarily a function of the number of smolts migrating to sea the previous year and their subsequent mortality rate at sea. A marine survival ratio index has been developed which is calculated as the number of adult salmon returning to the Gander River divided by the total juvenile salmon population in the Experimental Ponds Area (EPA) the previous spring used as an indicator of Gander River watershed smolt production. This survival index increased more than four-fold following closure of the commercial fishery in 1992 and has been used to predict adult salmon returns to the Gander River one year in advance (Ryan et al. 1995, 1996, 1997). The survival index provides a metric for estimating changes in mortality during the difficult-to-monitor marine phase of the life cycle. We previously presented data suggesting an apparent negative relationship between EPA juvenile abundance and the subsequent marine survival index (Knoechel et al. 1999). This relationship implies that there is an optimum range of juvenile abundance above and below which adult returns decrease. We herein present data indicating the density-dependent relationship was confirmed in 1999; the relatively low EPA juvenile abundance in spring 1998 was followed by a relatively high small adult return in 1999.

Methods

Juvenile salmon populations were assessed at the Experimental Ponds Area (EPA) which is located at the headwaters of the Northwest Gander River (Figure 1). Populations were estimated for Spruce Pond and Headwater Pond (Figure 2) using fyke nets and Schnabel multiple-mark-recapture methods as detailed by Ryan (1990). Headwater and Spruce ponds are shallow (mean depth 1.1 and 1.0 m, respectively), dilute (mean conductance 35 *u*S cm^{-1}), brown-water lakes whose physical and chemical characteristics have been detailed by Ryan and Wakeham (1984).

An adult counting fence has been operated continuously at the Salmon Brook fishway since 1978 and on the main stem of the Gander River since 1989. Total adult small salmon returns to the Gander River system have been calculated as the sum of the number passing through the fence and the number angled downstream of the fence. We have used adult return counts for both Salmon Brook and the whole river as updated by O'Connell et al. (2000).

Results and Discussion

The previously documented relationship between EPA juvenile abundance in the spring and small adult salmon returns to the Salmon Brook counting fence four years earlier, based on data from 1982-1994 excluding 1985 was: juveniles (year N) = (1.776 * Salmon Brook count (year N-4))+ 1468.36, (Ryan et al. 1997). This relationship predicted a spring 1999 juvenile abundance of 4310 based on the 1995 Salmon Brook count of 1600 small adults (Knoechel et al.1999). The actual spring estimate was 47% higher at 6322 (Table 1, Figure 3), just below the maximum of 6558 observed in 1996, thus the change was in the expected direction but of greater-than-expected magnitude.

A marine survival index, calculated as the ratio of total Gander River small salmon returns to EPA juveniles the previous year, indicated a major improvement in survival following the commercial fishing moratorium (Table 2). The mean survival ratio index during the first four post-moratorium years was 8.26 as compared to 1.71 in the two pre-moratorium years. Increased EPA juvenile abundances in 1995 and 1996 were followed by declines in the subsequent marine survival index estimates to 5.33 in 1996 and 1.60 in 1997, a level consistent with that observed prior to closure of the commercial fishery. EPA juvenile abundance declined in 1997 and the marine survival index subsequently increased to 6.04. These data demonstrated a negative correlation between juvenile abundance and subsequent marine survival consistent with an interpretation of density-dependent post-smolt mortality (Knoechel et al.1999). The least squares regression equation describing this relationship was:

Survival Index = 12.007 - (0.001564 * EPA Juvenile Estimate) Equation 1.
$r = -0.931$, $p = 0.002$, one-tailed test

Applying Equation 1 to the 1998 EPA juvenile estimate of 2385 fish yielded a predicted marine survival index of 8.277 which resulted in an expected 1999 return of 19,740 small adult salmon to the Gander River, very close to the actual return of 18,491 (McConnell et al., 2000). The actual return yields a 1999 Survival Index of 7.75 which further supports the negative correlation between EPA juvenile abundance and subsequent marine survival (Figure 4). Adding the 1999 data to the regression produces minimal change:

Survival Index = 11.843 - (0.001529 * EPA Juvenile Estimate) Equation 2.
$r = -0.931$, $p = 0.001$, one-tailed test

One potential criticism of this analysis is that it is based on a relatively short post-moratorium time span. There has been a strong correlation between whole river small adult returns and Salmon Brook small adult returns during the 11 years of overlapping operation. This suggests that it might be feasible to test for density-dependence over a longer time span by using the Salmon Brook adult returns as an index of whole-river returns. A plot of this Salmon Brook Survival Index (calculated as: Salmon Brook small adults year n+1 / EPA juvenile abundance year n) versus EPA juvenile abundance again reveals a highly significant negative relationship (Figure 5):

Salmon Brook Survival Index = 0.863 - (0.0001399 * EPA juvenile estimate) Equation 3.
$r = -0.777$, $p < 0.001$

This relationship is weaker than that for the post-moratorium period alone (Eq. 2 above) but this is to be expected given that there is variability in the correlation between Salmon Brook counts and whole river returns and given that there has been a wide range in commercial interception of returning adults during the past several decades.

The regression (Equation 3) can be used to predict Salmon Brook small adult salmon returns over a hypothetical range of EPA juvenile abundance estimates (Figure 6). The resulting dome-shaped curve shows a tendency to underestimate adult returns in the lower range of EPA juvenile abundance (Figure 7). It should be emphasized that both variables are proxies for broad-scale estimates; there is little chance that smolts produced from the EPA portion of the Gander River watershed actually contribute in a significant way to adult returns to Salmon Brook.

Continued monitoring of small adult returns to the Gander River in 2000 should provide a strong test of the robustness of the negative density-dependent relationship between EPA juvenile abundance and the subsequent Marine Survival Index. The near-record 1999 EPA juvenile estimate of 6322 leads to an estimated year 2000 Survival Index of only 2.18 (using Eq. 2) which, in turn, yields a predicted year 2000 small adult return to the Gander River of only 13,782 small adult salmon which is much less than the conservation requirement of 21,828 small spawners. If, on the other hand, the high Survival Index of 1999 persists (7.75, see Table 2) then the predicted small adult return would be 49,073, a record for post-moratorium years.

If the density-dependent marine survival pattern is confirmed, it would provide a scientific basis for refining recommendations regarding river management and it would provide a means of identifying periods of expected low marine survival which could then be the focus of research efforts into identifying the causes of mortality. If the prediction is refuted, then it would suggest the need for a further search for factors responsible for the apparent wide range in marine survival indices among years.

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Table 1. Spring Atlantic salmon juvenile population size in the Experimental Ponds Area (EPA, Spruce and Headwater ponds combined), Salmon Brook fishway small adult (<63 cm) counts, and Gander River small adult count.

Year of Census	Total Count EPA Juveniles	Salmon Brook Fishway Count	Gander River Total Small Salmon Count
1978		755	
1979	4822	404	
1980	3463	997	
1981	2393	2459	
1982	3077	1425	
1983	1603	978	
1984	3226	1081	
1985	3175	1663	
1986	4474	1064	
1987	3199	493	
1988		1562	
1989	4925	596	7743
1990	3642	345	7740
1991	2362	245	6745
1992	3069	1168	18179
1993	2470	1560	26205
1994	2370	963	18273
1995	4492	1600	22266
1996	6558	946	23946
1997	3112	465	10599
1998	2385	1295	18805
1999	6322	1105	18491

Table 2. Survival ratio indices calculated as the ration of returning Gander River small adult salmon to the EPA juvenile abundance the previous year.

Year of Census	EPA Juveniles (year n-1)	Gander River Return Small Adults (year n)	Survival Ratio Index (adults year n / juveniles year n-1)
1989			
1990	4925	7740	1.57
1991	3642	6745	1.85
1992	2362	18179	7.70
1993	3069	26205	8.54
1994	2470	18273	7.40
1995	2370	22266	9.40
1996	4492	23946	5.33
1997	6558	10599	1.62
1998	3112	18805	6.04
1999	2385	18491	7.75
		Mean Pre-closure Ratio (± S.E. for 1990-1991)	1.71 (± 0.20)
		Mean Post-closure Ratio (± S.E. for 1992-1995)	8.26 (± 0.90)
		Mean Post-closure Ratio (± S.E. for 1992-1999)	6.72 (± 2.43)

Figure 1. Gander River basin of insular Newfoundland with locations of study sites referred to in the text.

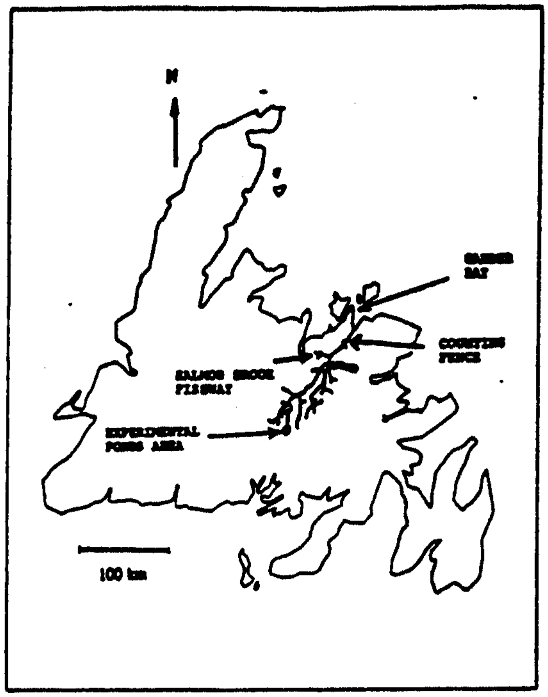
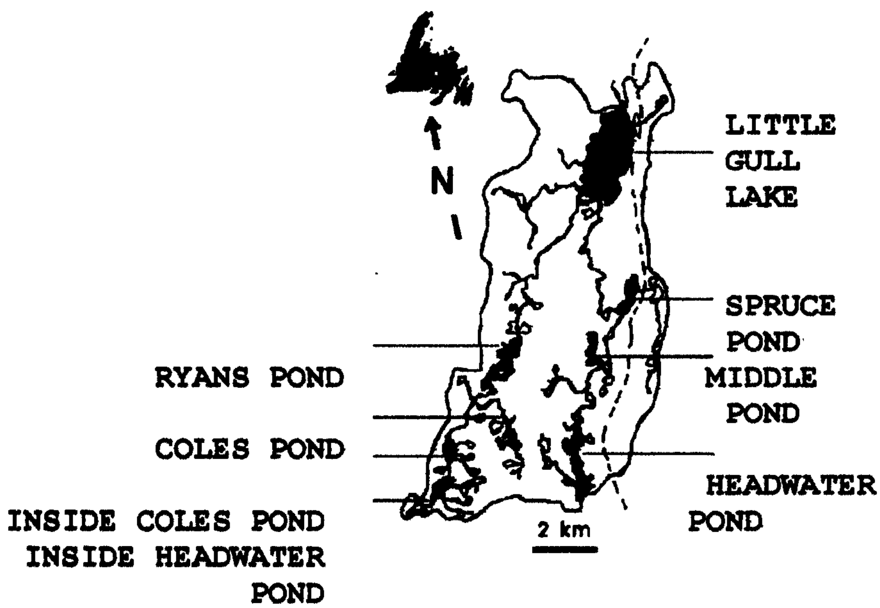


Figure 2. Watershed of the Experimental Ponds Area at the headwaters of the Northwest Gander River, central Newfoundland (inset). The dashed line through the east side of the watershed represents the Bay D'Espoir highway.



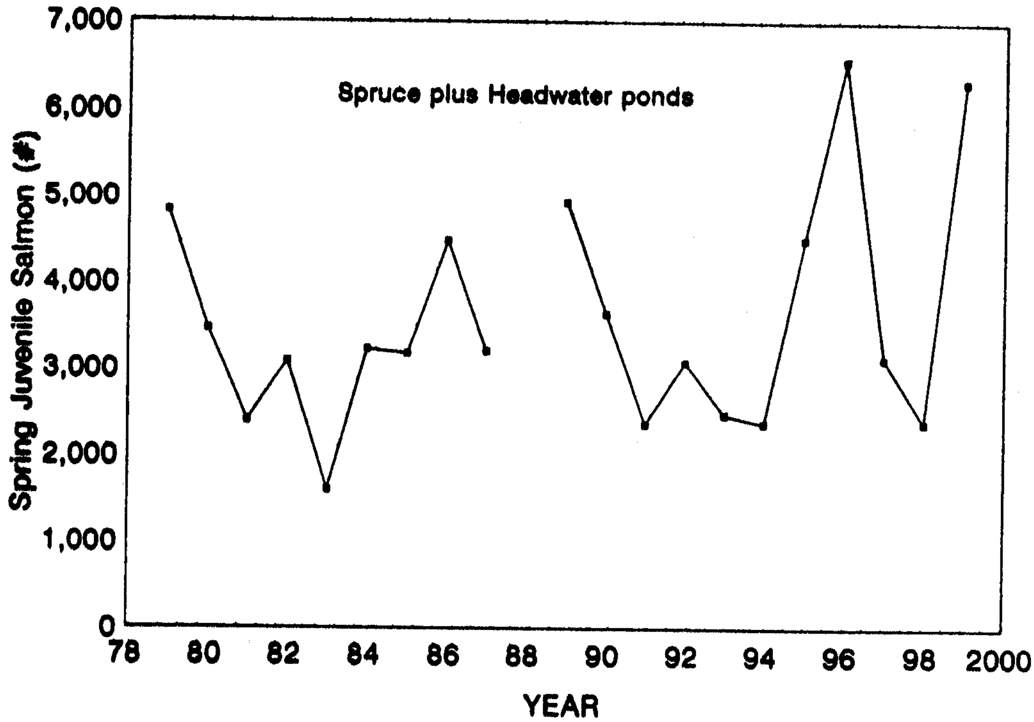


Figure 3. Spring Schnable population estimates of Experimental Ponds Area juvenile salmon (Headwater and Spruce ponds combined) from 1979 through 1999.

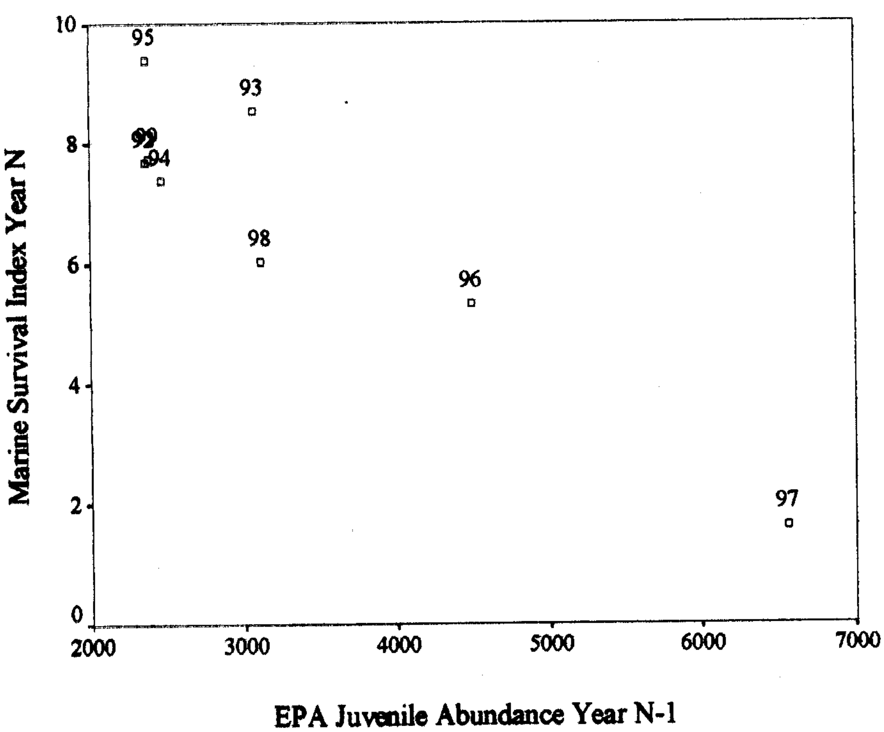


Figure 4. Relationship between estimates of the marine survival index and EPA juvenile abundance the preceding year for the post-moratorium period from 1992-1999. Year labels refer to the adult return year.

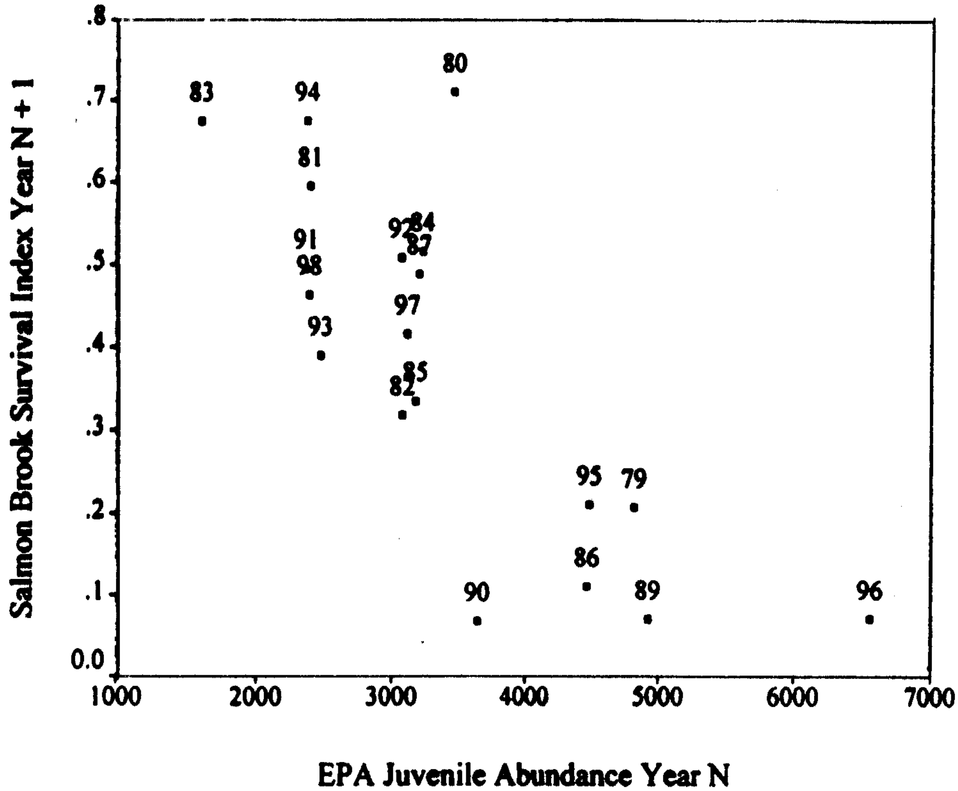


Figure 5. Relationship between EPA juvenile abundance in the spring and the Salmon Brook survival index calculated from the subsequent year small adult return for the period 1978-1999. Year labels refer to the juvenile estimate year.

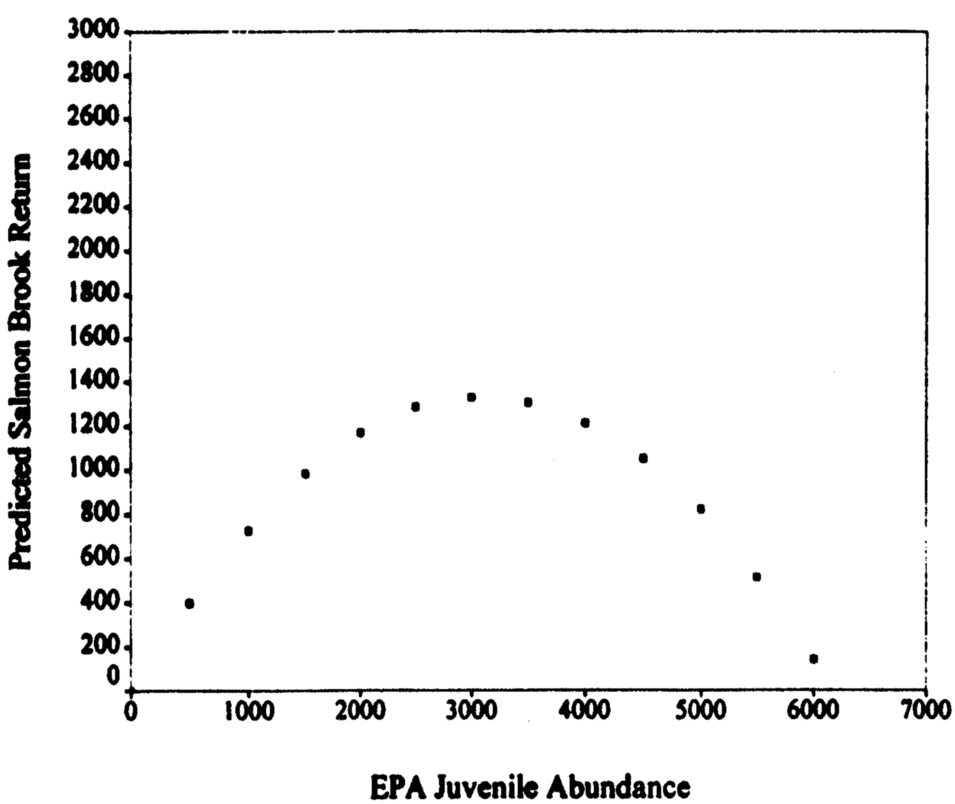


Figure 6. Relationship between small adult salmon returns to Salmon Brook and EPA juvenile abundance that would be predicted from Equation 3 describing the negative correlation between the Salmon Brook survival index and EPA juvenile abundance.

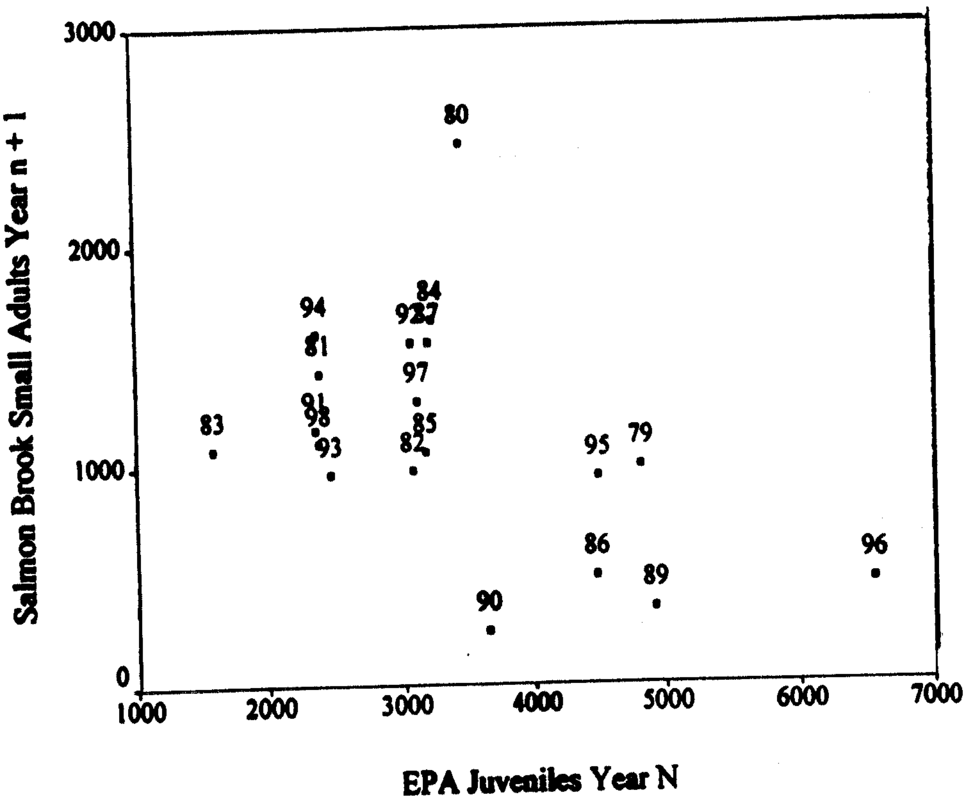


Figure 7. Observed relationship between spring EPA juvenile abundance and Salmon Brook small adult returns the subsequent year.