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# Recruitment of the North Amerlcan stock of Atlantic salmon (Salmo salar) relative to annual Indices of smolt production and winter habitat in the northwest Atlantic 

by

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#### Abstract

This document explores the utility of an index of annual production of the North American (NA) Atlantic salmon stock to test hypotheses of macro-level affects in the recruitment to fisheries and spawning escapement. Annual indices of smolt production are derived from Miramichi River presmolt densities relative to a measured maximum smolt production. The smolt production index is annually calibrated to the total NA stock using the relative performance of the Gulf of St. Lawrence one-sea-winter returns and the proportion that Miramichi returns were of the total NA one-seawinter (1SW) return. Recruitment models using smolt indices and winter habitat area explained high proportions ( 0.82 for one-sea-winter and 0.70 for multi-sea-winter salmon) of the variation in recruitment to distant fisheries, local fisheries and to spawning escapement. The addition of YEAR as a variable, suggested by trends in residuals, improved models to explain 0.86 and 0.93 of the variation in recruitment. Forecasts for recruits in 1997 to 1999 were derived using these regressions and simulation of values for proportions represented by the index and forecasts of habitat areas not available at forecast time. Most probable estimates of one sea-winter recruits were low for 1997 at $454 \times 10^{3}$ small salmon and increased to $522 \times 10^{3}$ in 1998. Modal estimates of multi-sea-winter salmon were very low in 1997 at $75 \times 10^{3}$, were similar for $1998,76 \times 10^{3}$ and were improved but low for 1999 at $105 \times 10^{3}$. Potential refinements to the model, ecological mechanisms implied from the analysis and implications for management of Atlantic salmon are discussed.


## Résumé

Le présent document traite de l'utilité d'un indice de la production annuelle du stock de saumon de l'Atlantique nord-américain pour le test d'hypothèses ayant trait aux effets, à un macro-niveau, sur le recrutement à la pêche et l'échappée de géniteurs. Des indices annuels de la production de saumoneaux sont obtenus des densités de pré-saumoneaux de la Miramichi par rapport à la production maximum mesurée de saumoneaux. L'indice de production de saumoneaux est étalonné pour chaque année en fonction du stock nord-américain total en utilisant le rendement relatif des remontées de poissons unibermarins (UBM) dans le golfe du Saint-Laurent et la proportion des remontées de la Miramichi par rapport aux remontées totales d'UBM du stock nord-américain. Des modèles du recrutement faisant appel à des indices fondés sur les saumoneaux et la superficie de l'habitat d'hiver expliquent les proportions élevées ( 0,82 pour les unibermarins et 0,70 pour les pluribermarins) de la variation du recrutement des pêches éloignées et des pêches locales et de l'échappée de géniteurs. L'ajout de l'année à titre de variable, comme semblait l'indiquer l'allure des résiduels, a permis d'améliorer les modèles et d'expliquer 0,86 et 0,93 de la variation du recrutement. Des prévisions du recrutement de 1997 à 1999 ont été obtenues à partir de ces régressions et de valeurs simulées pour les proportions correspondant à l'indice et aux prévisions des superficies des habitats non disponibles au moment de la prévision. Les estimations les plus probables de recrues d'unibermarins étaient faibles pour 1997, à $454 \times 10^{3}$ petits saumons, mais augmentaient à $522 \times 10^{3}$ pour 1998. Les valeurs modales estimées de saumons pluribermarins étaient très faibles pour 1997, à $75 \times 10^{3}$, semblables pour 1998, à $76 \times 10^{3}$, et quelque peu supérieures pour 1999, à $105 \times 10^{3}$. On traite d'améliorations pouvant être apportées au modèle, des mécanismes écologiques déduits de l'analyse et des incidences pour la gestion de saumon de l'Atlantique.

## Introduction

General declines in recruitment to rivers and fisheries among widely diverse stocks of wild Atlantic salmon, together with loss in freshwater habitat area producing seaward-migrating smolts, have resulted in widespread reductions in fishery exploitation in North American stocks of salmon. These reductions in fisheries have resulted in periodic increases in the numbers of salmon escaping to spawn (Figure 1) but without the anticipated increase in subsequent recruitment.

Juvenile salmon populations have increased in the remaining suitable habitat for many stocks. This response is especially true for those stocks with larger multi-sea-winter (MSW) salmon components (Ritter MS1997). Despite reduced fisheries, the numbers of recruits, i.e., spawners and harvests, have declined. Most disturbing (to some) is the fact that estimates of the number of pre-fishery salmon in the sea has declined to numbers approaching, or less than, those estimated for conservation of the stock (ICES 1997/Assess:10). Survival of hatchery-produced salmon (Harvie and Amiro, 1996) has also declined and is independent of the numbers of spawners, i.e., the number of migrating smolts is known.

Growing concerns have been raised that action must be taken to ensure the persistence of these stocks. The reality is, however, that few options remain to increase freshwater production. These actions include artificial propagation, habitat restoration, habitat expansion and productivity enrichment. Without a knowledge of the recruitment properties of the macro-stock there is an uncertainty that these methods will increase recruitment.

In light of this uncertainty the precautionary approach has been suggested as appropriate action to ensure persistence of the stock. The basic tenent of this policy is that, when faced with uncertainty about persistence of a population, reduce or at least do not increase exploitation. The efficacy of the precautionary approach is currently being reviewed and the results of its application for all states of nature and human actions remains to be evaluated.

Consequently, further reductions in the already low exploitation of Atlantic salmon (relative to earlier years when adult populations were higher and fisheries operated) are being called-out-for by some proponents at least until the salmon stocks recover. If we assume that recovery means increased adult salmon returns, then we need to know the factors that affect returns. If recovery means increased juvenile populations, then the goal has been achieved in many rivers, especially in rivers of higher productivity and without in-river loss factors i.e. acidification, fish passage, siltation etc.

Attributing cause to the decline in adult salmon recruitment and initiating appropriate and effective management strategy are 'systems approach' reactions intended to recruitment. However, the systems approach also suggests that before further action is taken the effects of recent changes in policy e.g. fixed or greater than conservation target spawing escapement, must be evaluated and the present condition of the stock and nature of the dynamic be determined before evoking new strategy.

Interpreting causes for the decline in apparent recruitment has been impeded by the lack of an indicator of the annual status of the total stock that accounts for the contribution that stock (spawners) makes to recruitment. Inclusion of lagged spawners (year i-5) as variable in a model of the North Atlantic salmon recruitment in year $i$, marginally increased the explained variance $\left(\mathrm{R}^{2}\right)$ from 0.68 to 0.71 (Anon. 1997). Therefore, the effect that increased escapements for the macro-stock of salmon have on subsequent recruitment has, to date, only been roughly modeled. Some over-estimates of the 1997 returns to some index stocks were, for the most part made from the assumption that documented increases in populations of spawners, juvenile salmon or smolts would result in increased recruits. These forecasts are based on the assumption of proportionate (with random error) marine survival with increasing smolt production.

The numbers of juvenile salmon and migrating smolts have been shown in Atlantic coast rivers to increase with increasing deposition of eggs and to compensate to a plateau by the sea-ward
migration stage at higher depositions. This compensation is based in both theory (Symons, 1979; Korman et al., 1994) and by observation (Elson, 1975; Buck and Hay, 1984). Similar observations have been made for steelhead trout (Oncorhynchus mykiss), a species with a similar life cycle as Atlantic salmon (Ward and Slaney, 1993). This plateau is the carrying capacity of the river for juvenile Atlantic salmon set by the biological constraints of competition and growth.

Instances where overcompensation (domed) curves have been applied to smolt production have been done without adequate explanation of the mechanism. In these cases, where stationarity in the habitat capacity was questionable, the incremental gain in accounted variance attributed to using the overcompensation model was not signifigant. Motivation for use of an overcompensation model is the ease of derivation of management parameters, such as maximum gain or maximum production, available from overcompensation models as opposed to compensation models.

Returns (recruitment) to the freshwater environment, however, are far less predictable. Data sets from rivers with enough resolution to interpret the form of the recruitment response suggest that marine survival is not linear. That is, the number of recruits decline relative to the number of spawners beyond some number of spawners. Combining the freshwater form of the stockrecruitment relationship together with non-linear marine survival yields an adult-to-adult or egg-toegg stock-recruitment response that is dome-shaped. This form of a stock-recruitment relationship has been termed "overcompensation" (Hilborn and Walters, 1992).

If one accepts a plateau form for the freshwater production response, the factor(s) necessary to result in overcompensation in an adult-to-adult stock-recruitment curve must be active during the marine migration stage. Mechanisms for this response have been suggested as, disease, cannibalism and oxygen limitation (usually freshwater effects), size dependent marine survival and marine predation. Because we have much evidence for the form of the freshwater relationship, marine survival relationships are key to explaining an Atlantic salmon stock-recruitment relationship. These forms of stock-recruitment relationships are known as multi-stage stockrecruitment models (Moussalli and Hilborn, 1986). Multi-stage models have been explored for some species of Pacific saimon but not extensively explored for Atlantic salmon.

Predator attraction may be described as a behavioural response that attracts and conditions predators to prey on a species depending on the relative presence of that species and the bioenergetics of utilizing that prey species. This response has been termed "depensatory" (Hilborn and Walters, 1992, p.262). If the predator is effective in accessing the prey, depensatory effects can result in stock-recruitment curves that have an overcompensation shape. Factors which affect the impact of the predator on the prey are principally the size of the predator population, coincident distribution with the prey, preference of the predator for that prey and efficiency of the predator to capture the prey. Examples of depensatory effects have been discussed for Pacific salmon species (Peterman, 1977 and 1980).

Inverse length (or weight) mortality has been estimated for Atlantic salmon (Doubleday et al., 1979). The form of the curve is logarithmic, and about $50 \%$ mortality has occurred by the end of month four and increases to $59 \%$ by the end of month eight. In this example, natural mortality slowly increased to $66 \%$ by month 24 (Fig. i, Appendix 1). Annual variation in early marine survival (e.g. Fig. ii, Appendix 1) in conjunction with later marine survival would have a multiplicative effect in the depensatory function. However, if early marine survival is inconsistent among sub-stocks, then variation in early marine survival alone cannot result in overcompensation in the macro-stock.

According to this model (depensatory effects at later marine stages) stocks will synchronize. Stock-recruitment of anadromous fish stocks (rivers or aggregations of rivers) which are regulated by the same set of predators acting on larger (older) fish will synchronize in recruitment where the levels of recruitment are determined by each stock's freshwater production. Predators acting on sub-sets of any grouping of stocks would contribute to variation in the relative performance of individual stocks. For a rapidly growing fish like salmon, the size vs. predator diversity effect results in less variation in natural mortality rate among stocks during the early marine stage (less
than four months) than at later stages. Thus, synchrony among non-adjacent stocks would not be expected to be significantly destabilized by relative abundance of one particular local predator preying on early migrating smolts. This expectation is because predator diversity is inverse to the size of the prey and for small fish, one predator is readily replaced by another. Synchrony among Atlantic salmon stocks has been previously documented ( Scarnecchia, 1983; Reddin and Shearer, 1987; Friedland et al., 1993).

In order for early marine survival to be significant in accounting for recruitment it would have to exceed the cumulative mortality value normally reached by the time when later stage predators begin the access to fish ( 0.57 by month seven). Variation in the proportion of the population consumed by predators at later stages of marine migration of salmon would readily de-stabilize any synchrony among stocks relative to small fish because there are fewer predators of larger fish. This mechanism underlies the inverse-weight mortality model. Fishing mortality is a prime example of a predator effect that can de-stabilize synchrony among stocks. Therefore, evidence of synchrony, especially on highly spatially divergent rivers (stocks), can be interpreted as exposure of the stocks to a common predator effect.

Many obstacles stand in the path of assessing stock-recruitment for individual rivers. Two major problems are: 1)That recruits, which were harvested in mixed-stock fisheries, cannot readily be attributed to specific index stocks, and 2) Variation in recruitment signals among stocks or groups of stocks attributed to random effects at later marine stages and variable local predation can give conflicting results.

If the total stock is undergoing stock-wide (macro) effects, then high production in any one stock cannot be expected to have a predictable response. Any identifiable change will depend on the level of the macro-stock. However, there is always a chance that large numbers of a particular stock will not be selected by the predator field even in an aggregated marine population. This effect would be enhanced if salmon migrate in stock-specific sub-aggregations.

To avoid these stock-specific complications (at the expense of taking on others) this paper explores the utility of using an index of annual production of the North Atlantic salmon stock to test hypotheses that macro-level affects and temporal changes in those effects account for variation and trends in annual recruitment to all North American Atlantic salmon rivers.

## Methods

An index of the total North American (NA) annual production of smolts was derived from the equation:

NA smolts yri $=$ Maximum smolt production rate of the Miramichi River * (( Pre-smolt index yri-1 / Proportion Pre-smolt index of maximum Pre-smolt index) / Proportion Miramichi one-sea-winter returns of total NA returns yri $1+1$ ))

Mirimichi pre-smolt indices were obtained from the equation:
Mirimichi pre-smoltsyri $=\left(\right.$ Density of age ${ }^{1+}$ parryri - Density of age ${ }^{2+}$ parryri+1 $\left.^{2+}\right)+$ Density of age $^{2+}$ parryri

Annual proportions that Miramichi one-sea-winter returns were of total NA returns were obtained from the equation:

Miramichi_prop $=(($ Estimate of maximum returns to Gulf + Estimated minimum returns to Gulf)/2) * Portion Miramichi salmon production area of the Gulf rivers

Estimates of returns to the "Gulf" portion of the Gulf of St. Lawrence were obtained from ICES Document 1997/Assess:10.

Salmon production area for the Miramichi River is $546,000 * 100 \mathrm{~m}^{2}$ units which is 0.5046 of the total Gulf salmon production area (O'Connell et al., 1997).

Smolts were estimated at maximum smolt production rates of 2.0 to 5.0 smolts $\mathrm{m}^{-2} * 100$. Sensitivity of the index of annual NA smolt production to maximum smolt production rate was assessed by reviewing the pattern of estimates obtained at the various rates. Accuracy of the total smolt estimate was assessed by comparison with values estimated for the Miramichi River 1951 to 1971 (Paloheimo and Elson, 1974).

Total recruits for each smolt cohort (smolt year) were obtained for sea-age 1 and sea-age 2 (one-sea-winter and two-sea-winter fish) using two methods:

Method 1.) Recruits were the sum of Pre-fishery estimates of the number of maturing salmon in $\mathrm{yr} \mathrm{i}+1$, the estimated Pre-fishery number of non-maturing salmon in $\mathrm{yr} \mathrm{i}+2$.

Method 2.)

- One-sea-winter recruits were the sum of estimates of returns of small salmon to home waters plus commercial catches of small salmon in yri+1 in Salmon Fishing Areas 1-7 and 14b in year $\mathrm{i}+1$ and SFAs 8 to 14a.
- Two-sea-winter (or more correctly multi-sea-winter salmon, because repeat-spawning salmon and three-sea-winter salmon were included in recruits of the cohort) were obtained from the sum of 2SW returns to home waters in yr i+2 of the smolt year; the commercial fisheries of Salmon Fishing Areas of large salmon in yr i+2 in Salmon Fishing Areas 1-7 and 14b, SFAs 8 to 14a, and the number of North American salmon in the West Greenland catch in $\mathrm{yr} \mathrm{i}+1$.

Estimated catches and returns were those reported by Anon (1997). No adjustment to standardize the recruits to a common temporal period was made.

North American Atlantic salmon stock annual Natural Mortality Rates were estimated from:
Natural Mortality $=$ Recruits/Smolts
Recruitment Rate of the total North American stock to all fisheries and escapement was derived as:

Recruitment Rate $=1$-Natural Mortality
Pre-fishery estimates of population abundance were those reported by Anon. (1997) and represent best estimates of the numbers of non-maturing salmon (potential two-sea-winter) in the North Atlantic prior to the West Greeniand Fishery and the numbers of maturing (one-sea-winter) salmon in the south Labrador Sea prior to commercial fisheries.

Indices of Atlantic salmon marine habitat area are those of Reddin and Freidland (1993) as reported by Anon. (1997) and D. Reddin (pers.comm.) ${ }^{1}$. Habitat indices for the months January, February, March and April were found by Reddin and Freidland (1993) to best account for variance in pre-fishery abundance of North American salmon in the North Atlantic Ocean. Returns of hatchery stocked smolts to three rivers of the Atlantic coast (Saint John, LaHave and Liscomb) have been shown to be significantly dependent on the values in most of these months, usually in the return year (Harvie and Amiro MS 1996). Indices for these months were shown to be highly correlated(lbid.).

[^0]
## Results

Pre-smolt densities for the time series 1972 to 1997 ranged from a low of $1.5 \mathrm{~m}^{-2} * 100$ in 1973 to a high of $35.1 \mathrm{~m}^{-2} * 100$ in 1995, (Table 1, Figure 2). Proportions that the Miramichi River was of the total North American one-sea-winter return ranged from a low of 0.061 in 1983 to a high of 0.204 in 1992 (Table 2, Figure 3).

## North American smolt production indices

Pre-smolt densities $\left(\mathrm{m}^{-2} * 100\right)$ and proportions estimated at a maximum smolt production of 3.5 smolts $\mathrm{m}^{-2} * 100$ resulted in estimates of the total North American smolt production ranging from a low of 814,054 in 1974, to a high of $16,423,785$ in 1996 (Table 3). Miramichi pre-smolt indices accounted for 0.67 of the variance in total North American smolt estimates (Figure 4).

## Sensitivity of smolt indices to smolt production rate

Sensitivity of smolt estimates to the maximum smolt production rate was highest in 1996, when smolt estimates ranged from a low of $9,385,020$ at 2.0 smolts $\mathrm{m}^{-2} * 100$ to a high of $23,462,550$ at 5.0 smolts $\mathrm{m}^{-2} * 100$ (Figure 5.) The pattern of annual North American smolts was similar for all maximum smolt production rates. Range in smolt estimates determined at 2.0 to $5.0 \mathrm{~m}^{-2} * 100$ was greater in high pre-smolt years than in low pre-smolt years.

## Calibrated smolt estimates

The total Miramichi River smolt runs, 1951 to 1971, were estimated by Paloheimo and Elson (1974) and ranged from 400,000 in 1969 to a $5,400,000$ in 1968. Three values over $5.0 \times 10^{6}$ occur in the data set. Two of these values were based on fewer than 100 recaptures and one year, 1965, was based on 194 tag recaptures. No estimates were based on a sufficient number of marks to obtain estimates with a coefficient of variation less than $50 \%$ at a population size of 200,000 let alone $5.0 \times 10^{6}$ (Ricker 1975). Estimates based on more than 20,000 tags applied and more than 500 recaptures had a maximum of $2.6 \times 10^{6}$ smolts or 4.76 smolts $\mathrm{m}^{-2} * 100$. Because analysis of effects and trends does not rely on an accurate calibration of the maximum smolt production rate, but rather the relative change in production, the median value of $3.5 \mathrm{smolts} 100^{-1}$ $\mathrm{m}^{2}$ was used for all analyses of effects and trends. Analyses dependent on the absolute number of smolts would be better served by using a maximum of 5.0 smolts $\mathrm{m}^{-2} * 100$ and would benefit from an independent method of estimating the maximum NA smolt production.

Pre-fishery estimates vs. total North American smolts
Regression of Pre-fishery estimates of non-maturing (1SW) salmon on annual estimates of the number of smolts was significant ( $\mathrm{p}=0.014$ ) with an $\mathrm{R}^{2}=0.244$ (Figure 6). Pre-fisheries estimates of maturing (MSW) salmon did not have a slope significantly different from $0(\mathrm{p}=0.525)$.

## Estimates of recruits

Recruits by Method 2 were greater than the estimate of smolts in 1974 (Table 3). Rather than attempting to resolve this apparent discrepancy the 1974 smolt cohort was excluded from the analysis.

Recruitment rate determined from Pre-fishery estimates (Method 1) were similar and sometimes greater than those determined from catches (Method 2; Figure 7.) Differences in the recruitment rate between the two methods were generally greater in high recruitment rate years than in low recruitment rate years. The correlation coefficient was 0.9898 between the rates determined by the two methods. Recruitment rates from pre-fishery numbers ranged from a low of 0.062 recruits smolt ${ }^{-1}$ in 1995 to a high of 0.82 in 1985. Recruitment rate from catches ranged from a low of 0.04 in 1993 to a high of 0.56 in 1985.

## Natural mortality of North American smolts

Natural mortality was defined as (1-Recruitment) and therefore showed the same pattern as recruitment rate. Natural mortality estimates derived at 3.5 smolts $\mathrm{m}^{-2} * 100$ by Method 1 ranged from a low of 0.45 in 1985, to a high of 0.938 in 1995 (Table 3). Natural mortality values for Method 2 ranged from a low of 0.44 in 1985 to a high of 0.96 in 1993. (Values for 1995 smolt cohorts cannot be estimated until returns in 1997 are tallied).

Sensitivity of natural mortality rates to maximum smolt production values Sensitivity of natural mortality rate to the maximum production rate used in a determination was highest in 1985 and 1986 when natural mortality rates ranged from a low of 0.034 at 2.0 smolts $\mathrm{m}^{-2} * 100$ to a high of 0.57 at 5.0 smolts $\mathrm{m}^{-2} * 100$ (Figure 8). The pattern of annual North American natural mortality rates was similar for all values of maximum smolts. The range of mortality rates determined at 2.0 to $5.0 \mathrm{~m}^{-2} * 100$ was greater in low pre-smolt years than in high pre-smolt years.

## Form of natural mortality curves

Natural mortality was curvilinear rather than linear with the number of smolts estimated for any value of maximum smolt production rate used (Figure 9). This suggested a natural log conversion of the smolt numbers was appropriate for analysis by general linear regression (Systat 7.0) ${ }^{2}$.

Slopes of the regression:
Natural mortality $=\alpha^{*} \operatorname{Ln}($ Smolt estimate $)-\beta$
were higher at low maximum smolt production rates than at high maximum smolt production rate. Parameter values $(\alpha, \beta)$ at maximum production of 3.5 smolts $\mathrm{m}^{-2} * 100$ obtained for this model were used to estimate expected total returns (1SW yr $\mathrm{i}+2 \mathrm{SW}$ yr $\mathrm{i}+2$ ) from annual smolt estimates. Expected Total Recruits were estimated as:

> Total Recruits = Smolt estimate * Natural Mortality

The residuals for this model showed a strong negative temporal trend (Figure 10).

## Recruitment and winter habitat indices

The residuals of the Total Recruits $=($ Smolt*Mortality) were correlated with all four winter habitat indices in smolt yr i+1 (Figure 11) or smolt yr i+2 (Figure 12).

This analysis suggested multiple regression models of the form:
and
1SW Recruits $=$ Ln(Smolts) + Habitat + Constant + error
MSW Recruits $=\operatorname{Ln}($ Smolts $)+$ Habitat + Constant + error
Regression analyses were conducted using forward-step multiple regression with an F-to-enter of 0.10 and an F-to-remove of 0.10 for Habitat values for January to April of $\mathrm{yr}+1$ (LHBTxxx) and Habitat values for January to April of yri+2 (L2HBTxxx) of the smolt year were used to reduce the number of variables in the models.

[^1]
## One-Sea-Winter recruit models

Stepwise regression retained LNSMOLT and LHBTFEB and was significant. Regression statistics for the 1SW model were:

Dep Var: ISW_RECRUITS N: 23 Multiple R: 0.73430 Squared multiple R: 0.53919
Adjusted squared multiple R: 0.49311 Standard error of estimate: $1.25574 \mathrm{E}+05$

| Effect | Coefficient | Std Error | Std Coef Tolerance |  | $t$ | $P(2$ Tail) |
| :--- | :---: | :--- | :--- | :--- | :--- | :--- | :--- |
| CONSTANT | $2.62656 E+06$ | $8.75909 \mathrm{E}+05$ | 0.0 |  | 2.99867 | 0.00710 |
| LNSMOLT | $-1.70958 \mathrm{E}+05$ | 54685.79594 | -0.47517 | 0.99730 | -3.12619 | 0.00532 |
| LHBTFEB | 389.52799 | 110.52246 | 0.53570 | 0.99730 | 3.52442 | 0.00213 |

Analysis of Variance

| Source | Sum-of-Squares | of | Mean-Square | F-ratio | P |
| :--- | :---: | :---: | :---: | :--- | :--- |
| Regression | $3.69028 \mathrm{E}+11$ | 2 | $1.84514 \mathrm{E}+11$ | 11.70113 | 0.00043 |
| Residual | $3.15378 \mathrm{E}+11$ | 20 | $1.57689 \mathrm{E}+10$ |  |  |


| Durbin-Watson D Statistic | 1.412 |
| :--- | ---: |
| First Order Autocorrelation | 0.282 |

The residuals of this model showed a temporal trend.


A new variable YEAR, a simple metric vector, in this case the value for smolt year, was added to the model. The variable was not significant ( $\mathrm{p}=0.518$ ).

Visual inspection of the residuals of the 1SW model show no trend in the residual pattern prior to 1979 and a declining trend from 1979 to 1995.

The regression model for the 1979 to 1995 period without YEAR was highly significant ( $p<0.000001$ ) and accounted for 0.825 of the variance in 1 SW recruits for the period 1979 to 1995. Summary statistics for this regression were:

Dep Var: ISW_RECRUITS N: 17 Multiple R: 0.92040 Squared multiple R: 0.84714
Adjusted squared multiple R: 0.82530 Standard error of estimate: 80340.60456


The addition of YEAR as a variable to the 1979 to 1995 sub-set resulted in significant ( $p<0.000001$ ) regression which accounted for 0.868 of the variation in 1SW recruits

Dep Var: ISW_RECRUITS N: 17 Multiple R: 0.94478 Squared multiple R: 0.89261
Adjusted squared multiple R: 0.86783 Standard error of estimate: 69881.66603


[^2]
## Multi-Sea-Winter recruit models

Stepwise regression retained LNSMOLT and LHBTMAR. The model was significant ( $p<0.00001$ ) and accounted for 0.705 of the variance in MSW recruits. Regression statistics for the MSW model were:

Dep Var: MSW_RECRUITS N: 22 Multiple R: 0.85632 Squared multiple R: 0.73328
Adjusted squared multiple R: 0.70521 Standard error of estimate: $1.02791 \mathrm{E}+05$

| Effect | Coefficient | Std Error | Std Coef | Tolerance | $t$ | $P(2$ Tail) |  |
| :--- | :---: | :--- | :--- | :--- | :--- | :--- | :--- |
| CONSTANT | $1.68050 \mathrm{E}+06$ | $7.72755 \mathrm{E}+05$ | 0.0 |  | 2.17469 | 0.04249 |  |
| LNSMOLT | $-1.44814 \mathrm{E}+05$ | 50609.23744 | -0.34351 | 0.97407 | -2.86142 | 0.00999 |  |
| LHBTMAR | 579.41557 | 82.64305 | 0.84166 | 0.97407 |  | 7.01106 | 0.00000 |

Analysis of Variance

| Source | Sum-of-Squares | df Mean-Square | F-ratio | P |  |
| :--- | ---: | ---: | ---: | :--- | :--- |
|  |  |  |  |  |  |
| Regression | $5.51924 \mathrm{E}+11$ | $22.75962 \mathrm{E}+11$ | 26.11819 | 0.00000 |  |
| Residual | $2.00752 \mathrm{E}+11$ | 19 | $1.05659 \mathrm{E}+10$ |  |  |

Durbin-Watson D Statistic 1.147
First Order Autocorrelation 0.395

Residuals from this model showed a declining temporal trend.
MSW Residuals vs Year


The addition of a YEAR variable to this model resulted in a significant ( $p<0.000001$ ) model which accounted for 0.851 of the variation in MSW recruits. The regression statistics for this model were:

Dep Var: MSW_RECRUITS N: 22 Multiple R: 0.93416 Squared multiple R: 0.87265
Adjusted squared multiple R: 0.85142 Standard error of estimate: 72975.13819

| Effect | Coefficient | Std Error | Std Coef | Tolerance | $t$ | P (2 Tail) |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| CONSTANT | $3.59455 \mathrm{E}+07$ | $7.73999 E+06$ | 0.0 |  | 4.64412 | 0.00020 |
| LNSMOLT | -1.22387E+05 | 36283.14337 | -0.29031 | 0.95518 | -3.37311 | 0.00339 |
| LHBTMAR | 249.45033 | 94.70940 | 0.36235 | 0.37382 | 2.63385 | 0.01685 |
| YEAR | -17181.95406 3871.41054 | -0.60309 | 0.38316-4.43816 | 0.00032 |  |  |

Analysis of Variance

| Source | Sum-of-Squares | di Mean-Square | F-ratio | P |
| :--- | :--- | ---: | :--- | :--- |
|  |  |  |  |  |
| Regression | $6.56820 \mathrm{E}+11$ | $32.18940 \mathrm{E}+11$ | 41.11262 | 0.00000 |
| Residual | $9.58567 \mathrm{E}+10$ | 18 | $5.32537 \mathrm{E}+09$ |  |

*** WARNING ***
Case $\quad 6$ is an outlier $\quad$ (Studentized Residual $=-4.74651$ )
Durbin-Watson D Statistic 2.071
First Order Autocorrelation -0.58
Case 6, the 1977 smolt year, was a significant outlier to the model indicating further error reduction could be achieved by dropping this point or reducing its weight in the model. For exploration purposes the model was estimated without the 1977 point. The model without YEAR was significant ( $p<0.000001$ ) and accounted for 0.705 of the variation. Regression statistics for this model were:

Dep Var: MSW_RECRUITS N: 22 Multiple R: 0.85632 Squared multiple R: 0.73328
Adjusted squared multiple R: 0.70521 Standard error of estimate: 1.02791E+05


Addition of the YEAR variable to the model (without 1977) was significant ( $p<0.000001$ ) and the model accounted for 0.935 of the variation in MSW recruits.

Dep Var: MSW_RECRUITS N: 21 Multiple R: 0.97194 Squared multiple R: 0.94466
Adjusted squared multiple R: 0.93490 Standard error of estimate: 49243.79753


Durbin-Watson D Statistic 1.745
First Order Autocorrelation 0.088
The residuals from this last model showed no significant trends with the increasing values of the estimate or with increasing year.


## Calibrated estimates and parameter interpretation

Running this analysis at a calibrated maximum smolt production value of 5.0 smolts $100^{-1} \mathrm{~m}^{2}$ quantifies as well as indicates the trend in changes to recruitment after adjusting for the stock and habitat effects. Estimates derived at 5.0 smolts $\mathrm{m}^{-2} * 100$ and without the 1977 smolt class have the same parameter values as the 3.5 smolts $\mathrm{m}^{-2} * 100$ model with the exception of the intercept. For MSW recruits at the 5.0 smolts maximum, the intercept was $35.7 \times 10^{6}$ smolts. This is the maximum value of wild smolts in the North Atlantic that are accounted for in the non-maturing component. The 1SW recruit model using the data after 1978 and with smolts at the maximum of 5.0 smolts $100^{-1} \mathrm{~m}^{2}$ had an intercept of $21.7 \times 10^{6}$ smolts. If all production units produced 5.0 smolts $100^{-1} \mathrm{~m}^{2}$, then the sum of the two intercepts or $57.4 \times 10^{6}$ smolts is an estimate of the maximum smolt production in the North Atlantic during this period. An alternate method to obtain an estimate of the maximum smolt production is to use Total Recruits in a combined recruitment
model. This analysis, Total Recruits $=\operatorname{Ln}($ Smolt 5$)+$ LHBTFEB without the 1977 year class, accounted for 0.867 of the variation and had an intercept value of $52.29 \times 10^{6}$ smolts.

Parameters for other variables in the models show the rate of increase or decrease in the number of recruits per unit increase in that variable. For instance, for every unit increment in the log of the number of smolts (LnSmolts) there is a loss of 87,978 MSW recruits: for every unit increment in habitat area there is a gain of 296 MSW recruits; for every year since 1972 there has been an average loss of 17,365 MSW recruits. This is the average loss per year after accounting for the stock effect and the habitat effect.

## Forecasts

Forecasts of recruits to all North American fisheries and escapement were done through regression and simulation. Simulation was required because the 1997 proportion that Miramichi River represents of the total NA stock has not yet been determined and the 1998 habitat values are not yet known. Highest $R^{2}$ (adjusted) models were used to forecast returns in and 1998 for 1SW and MSW returns in 1997, 1998 and 1999.

Habitat values for February 1998 were estimated by regression of L2HBTFEB (yri+2 of smolt) on LHBTxxx(yr $\mathrm{i}+1$ of smolt) in a stepwise regression model. The best predictor of L2HBTFEB was LHBTAPR. The equation was;

$$
\text { L2HBTFEB }=1.06670 * \text { LHBTAPR }-106.37
$$

with $n=24, R^{2}=0.7443, p<0.000001$ and a Standard error of the estimate of 121.699. These parameters and standard error of the estimate allow the forecast using random selection of possible values from the normal distribution of LHBTFEB1 $1_{1998}$ forecasts for the predictor LHBTAPR1 $_{1997}$ value of 1714(Neter et al. 1996).

Values for LHBTMAR were similarly obtained where the best predictor of L2HBTMAR was LHBTMAR. The equation was;

$$
\text { L2HBTMAR }=0.85716 \text { * LHBMAR }+211.36
$$

with an $n=24, R^{2}=0.7418, p<0.000001$ and a standard error of the estimate of 136.874 .
Smolt indices for 1996 and 1997 are partially derived from 1SW returns in 1997 and 1998. Therefore, a range of possible SMOLT5 (Table 4) values for 1996 and 1997 was obtained by simulation analysis where the value for the proportion of Miramichi one-sea-winter returns of the Gulf returns in the equation was selected at random from the normal distribution of the mean and standard deviation observed in the data ( $0.11636 \pm 0.0382$ ).

Smolt estimates derived at a maximum smolt production of 5.0 smolts $\mathrm{m}^{-2} * 100$ were used in the forecasts(LNSMOLT5).

## 1SW Forecasts

Estimates of 1SW recruits for 1997 derived from 500 projections indicate a low recruitment in 1997 (Table 5). The modal value for 1SW forecasts in 1997 was 454,562 and the mean (similar to the deterministic forecast) was lower at $441,8701 \mathrm{SW}$ recruits. This level of recruits, while low, is not the lowest in the time series of recruitment to the North American stock (Figure 1). The 5th and 95th percentiles of projections were 379,213 and 485,888 1SW recruits. Estimates of 1SW recruits for 1998 indicate increased recruitment. The mean was 563,443 the mode was 522,807 and the 5th and 95th percentiles were 425,206 and 701,457 1SW recruits in 1998. Graphic presentation of the simulations follow.


Simulation forecasts for 1997 and 1998 1SW recruitments.
MSW Forecasts
The mean estimate of MSW recruits for 1997 was 62,680 salmon (Table 5). The modal value was higher at 75,511 and the 5th and 95th percentiles were 51 and 105,890. Forecasts for 1998 were similar to those for 1997 with a mean of 59,732 , a mode of 76,073 , and 5 th and 95 th percentiles of 0 and 103,756 MSW recruits in 1998.


Simulation forecasts the 1997 and 1998 MSW recruitement.


Simulation forecast for the 1999 MSW recruitment.
Forecasts of MSW recruits in 1999 increased. The mean estimate was 89,790 MSW recruits the modal estimate was 105,294, and the 5th and 95th percentiles were 0 and 168,900.

## Cross validation

The utility of the smolt and habitat data to derive deterministic forecasts of 1 SW and MSW recruits was examined through $n-1$ cross validation. Each year in succession from 1979 to 1995 for 1SW and 1972 to 1994 for MSW was omitted from the determination of regression parameters and a forecast for that year determined using these interim parameters. The mean and $90 \%$ confidence intervals of the estimate were plotted against the observed value (Figures 13 and 14). No observations fell outside the $90 \%$ bounds for 1SW forecasts although two cases were close to the $5^{\text {th }}$ percentile estimate (Figure 13). One forecast, that for 1983, was outside the $5^{\text {th }}$ percentile (Figure 14). This analysis indicated that for the observations made in this period forecasts were likely to include the observation and where observations were at the extremes of the forecasts it was more likely to underestimate than to overestimate the observation.

## Evidence of Predator effects

This analysis was predicated on the hypothesis that later marine mortality, at least after four months, would have a significant affect on the number of recruits. The analysis suggests that month seven to month eight after smolt migration has a large effect on the number of recruits. Loss of salmon at this stage can be attributed to large predators, including fishing mortality. The outcomes of almost all possible fates of salmon at sea can for the most part be interpreted from data gleaned from cohort survivors.

The inverse weight estimate of cumulative natural mortality was 0.55 after month six and 0.66 after month 24 (Appendix 1). At 5.0 smolts $\mathrm{m}^{-2} * 100$ there was a maximum of $23.4 \times 10^{6}$ (Table 4) smolts migrating in 1996. About $12.8 \times 10^{6}$ would still be alive after month six and estimated recruitment of all sea ages of adults for this smolt class is 506,982 . Without accounting for average natural mortality in the return migration months, a maximum of $12.3 \times 10^{6}$ salmon will be unaccounted for in the 1996 smolt class. Losses at sea of these magnitudes attributed to undetected fishing mortality is highly unlikely. Therefore, the fish: 1)are still at sea and will return in a later year, 2) died and fell to the bottom of the ocean (wasted), or 3) have fallen victim to predators.

Apparently few three-sea-winter salmon and fewer four-sea-winter salmon are present in the North American salmon stock. Therefore, later (delayed) maturity does not explain the loss in recruitment.

If fish died and fell to the bottom and were wasted, we will never know. This is an unlikely event in marine ecosystems. Given that most mass mortality 'fish kills' result in large numbers of floating casualties and in subsequent aggregations of scavengers, fish kills of this magnitude over this period of time, 1972 to 1995, would likely have been observed at some time. No such observation has been reported.

The third possibility is the fish were preyed upon. If this were the case, then there is a possibility that some signal was contained in the survivors. The result of a population undergoing active reduction by predators could be some form of selection. This selection may be size-dependent. The main survival feature of salmon is swimming speed and swimming speed is a function of length. If many salmon were lost to predators after the six-month time period, then there may be some selection against smaller fish. This signal would be present in the survivors.

Mean length and weight of LaHave River age-2.1 wild salmon was high in 1973 and 1986 and low in 1978 and 1979 (Figure 15). Neither mean length, modal length, coefficient of skewness nor condition factors of age 2.1 wild grilse were correlated with LaHave return rate of 1SW hatchery fish nor with mortality of North American smolts. Patterns were suggestive of relationships but no statistical relationships were found. Coefficient of skewness in lengths of age 2.1 wild salmon at Morgan Falls fishway, LaHave River, was shown to have a significant ( $p=.007$ ) positive trend over the 1976 to 1997 period (Amiro et al. in prep).

## Discussion

The use of Miramichi River pre-smolt and Gulf of St. Lawrence returns seemed an optimistic exploration. Based on production area alone, these rivers are only 0.23 of the total North American recruitment. That area is however in the middle of the North American habitat production range and the data have been collected with sound protocol and for a long period. The analysis may benefit from the addition of more indicator rivers, such as a major north shore river of the Gulf of St. Lawrence, but, whatever indicators are added, the total production area for North American salmon would remain the same and the total smolt production is not likely to change substantially. This expectation is because production is adjusted annually by the proportion that Gulf fisheries were of the total North American return and the same procedure would have to be used for additional indicators. For most of this analysis the pattern of change in the stock component was more important than the absolute accuracy of the estimate.

The pre-fishery forecast model of Reddin et al. (1993) is essentially a recruitment (pre-fishery abundance) model based on winter habitat without a stock variable. Attempts to use spawners as a signal for stock did not significantly (10\%) increase the R $^{2}$ of the models (ICES CM 1996 Assess:11). The wide range in age-at-smoltification in the North American stock is difficult to account for in an adult-to-adult stock-recruitment model.

Models presented here which included smolt indices increased the proportion of the explained variance by $13 \%$ for 1SW salmon recruits and $15 \%$ for 2SW salmon recruits from models using only recruits and winter habitat. (Increases in accounted variance also hold true when a YEAR variable is added to single variable habitat models for 1SW and 2SW.) Without the YEAR variable included these analyses provide residuals adjusted for stock and habitat for either 1SW recruits or 2SW recruits. The residuals provide a pattern of gains and losses which may be associated with some other marine effect. Increases in accounted variation of this magnitude are reason enough to include smolt estimates in further explorations.

The YEAR variable in the models represents some changing condition that has negatively affected the recruitment of 1SW salmon since 1978 and MSW fish for the complete time series of data explored here ( 1972 to 1994 smolt years). There is a tolerable but high serial correlation in the models (Durbin-Watson values approaching 2), which indicates that there is a strong monotonic trend in the data.

Using YEAR in forecast models was the only variable available to account for the negative trend in recruits. YEAR will continue to improve the $R^{2}$ of the models as long as the trend in lower marine survival continues. YEAR cannot forecast a turn-around in marine survival, it is a simple metric vector. Improved marine survivals in the future will erode the YEAR effect. Therefore, if stable forecast models are required, then the YEAR variable must be replaced.

The increase in skewness in lengths of age 2.1 grilse of LaHave River (Table 6) is suggestive that loss to predators is the cause of lower marine survival (Amiro et al. in prep). This decline in survival is associated with marine habitat in months seven and eight of the smolt migration. An alternate hypothesis may be that the monotonic increase in length, condition factor and skewness of age 2.1 salmon since 1984, is a result of changes in the marine harvest of Atlantic salmon. Major shifts in the harvests of salmon were effected by Salmon Management Plans of 1983, 1984 and 1992. The 1983 plan, which called for no legal by-catch of salmon would most affect the size and recruitment of one-sea-winter salmon to the LaHave River. The data show that periodic increases in mean lengths occur as far back as 1974 and 1975, while these fisheries were active (Figure 15).

Tagging (Ritter 1989), marine sampling (Reddin 1988a) and random walk modeling (Anon. 1994) indicate salmon are in the south Labrador Sea at this time. Aggregations of large, efficient, predators acting on the total stock of North American salmon at this time and location could explain the synchrony in recruitment in the North Atlantic stock.

Potential known predators of salmon in that area at these times are marine mammals (principally seals), large pelagic feeding fish and large fish-eating oceanic birds. Populations of large fisheating fishes in that area are low relative to historic populations. Populations of large oceanic birds are not known to be high in that area at that time. The populations of the three principal species of seals are known to have increased greatly during the range of years examined here (Anon. 1996). Populations of other marine mammals that utilize Atlantic salmon are unknown. Examining data of the time series of these populations and uncovering direct evidence of predation on salmon, is an important next step in examining potential replacements for the marine HABT(habitat) and/or YEAR effect in the salmon models.

Ecological theory suggests that both predator and prey have life history strategies that maintain population persistence. This concept is contained in the predator attraction theory for the predator and the compensatory feature of the stock-recruitment response. Bcth strategies have been destabilized by anthropomorphic actions. Some predators have been harvested in large numbers since human occupation of the lands abutting the North Atlantic (e.g. seals, Anon. 1996). Prior to the closing of the seal harvest the last remaining significant predator of salmon, humans, have reduced their fishing mortality substantially. Fishing mortality of salmon is but a fraction of that practiced for at least two hundred years. These reductions in fishing mortality have increased escapements of salmon to the highest recorded in 1981 and 1988. Recruitment from these yearclasses was less than the spawning escapements that contributed to them and harvests were lowest (Anon 1997).

In pre-colonization times salmon and predators would have interacted according to the above mechanisms to a relative equilibrium. If the predator effect was only at the marine stage then this equilibrium would have been highly oscillatory. If predator effect on adult salmon in the freshwater were independent of the marine environment, then a far more even pattern of recruitment (equilibrium) is attainable.

## Two-stage stock-recruitment

A stock-recruitment simulation model was used to demonstrate the effect of marine and freshwater stage predator effects on recruitment stability. A two-stage stock-recruitment model for the North Atlantic stock of Atlantic salmon was derived using the Beverton-Holt model for smolt production and two separate marine mortality models: E) a semi-logarithmic form and L) a logistic form. These models were suggested both from theory and from examination of the data.

The Beverton-Holt model used for smolt production requires two parameters: 1)The maximum smolt population and 2) the number of smolts produced per spawner in the linear portion of the curve. A maximum of $55.0 \times 10^{6}$ smolts was used, as suggested from the earlier analysis. A rate of 25 smolts per spawner, similar to that in Miramichi River as an expectation of 5.0 smolts $\mathrm{m}^{-2}$ * 100 and the conservation escapement.

Parameter values for the semi-log function ( E ) were estimated from the mortality curve at 5.0 smolts $\mathrm{m}^{-2} * 100$ (Figure 9). These values were used to derive the first set of simulated recruits (Figure 16).

A logistic survival curve ( L ) of the form;

$$
\text { Mortality }=\mathrm{C}^{*} \text { Population at } 0.5 \text { mortality } / \mathrm{A}^{\mathrm{B}}+\text { Population at } 0.5 \text { mortality }
$$

was used to generate the second set of simulated recruits (Figure 17). The logistic curve had three parameters :1) the population at which half the maximum mortality occurs $(A), 2)$ the slope or rate of increase in mortality $(\mathrm{B})$ and 3 ) the maximum mortality expected( C$)$. The mortality curve at the 5.0 smolts $\mathrm{m}^{-2} * 100$ rate reached 0.5 mortality at $4.44 \times 10^{6}$ smolts and this value was used for the $C$ parameter of the logistic curve. A value for ( $B$ ) of 2.55 was used in the analysis and was derived from the non-linear fit of the model to the recruitment data and smolt data at 5.0 smolts $\mathrm{m}^{-}$ ${ }^{2}$ * 100 and the parameter values for A and C as mentioned.

Discrete values of recruits were derived from the above models over a range of 0 to $>1.0 \times 10^{6}$ spawners. These sets of stock and recruits were used in a stock recruitment simulator
model(Atlantic Salmon Target Escapement Risk Analysis, ASTERA) to evaluate the effect of target escapement and fixed exploitation policies on recruitment. ASTERA is a forwardaggregating population simulator that can evaluate the impact of policy (management rules) on the stability of recruitment. The model allows set values of variance in environment (procedural error), management error and serial correlation in the environment (Rho) effects.

In order to carry populations forward (years) the model requires the habitat area, absolute fecundity (eggs $*$ fish $^{-1}$ ) and partial recruitment values to spawning. For the purposes of this analysis the habitat area for the North American stock was set by the formula;

Area $=\left(1996\right.$ total smolt estimate at 5.0 maximum smolts $\left.\mathrm{m}^{-2} * 100 / 5.0\right) * 100$ or $469,251,000 \mathrm{~m}^{2}$ of habitat.

Eggs*fish ${ }^{-1}$ was 3079, the LaHave river value used in the Atlantic Salmon Regional Acidification Model (Korman et at. 1994).

Partial recruitment values for total age past the spawning year were:

| year 4 | year 5 | year 6 | year 7 | year 8 | year 9 |
| :--- | :--- | :--- | :--- | :--- | :--- |
| 0.15 | 0.30 | 0.30 | 0.10 | 0.10 | 0.05 |

Partial recruitment rates for the North Atlantic stock have not previously been estimated. Values for partial recruitment were chosen to represent the age classes 3.1 (freshwater age.sea age), 2.2, $2.3,3.2$ and 4.1 in years five and six from the return year which are the age classes of the majority of the salmon recruits to North America.

Environment error was set at 0.25 which is the portion of the unexplained error in the MSW models without YEAR. Simulations were run assuming no management error and no serial correlation in the recruitment. Simulations were run for 110 years.

Simulation analyses were run to evaluate the effect of management policies on recruit stability. Policies evaluated were: 1)perfect fixed escapement management where all recruits in excess of a management target escapement ( 240 eggs $\mathrm{m}^{-2} * 100$ ) are harvested and 2) fixed exploitation of 0.10 .

The results show recruitment well in excess of the target for a fixed escapement policy where all recruits in excess of the target are harvested. When minimum exploitation was applied recruitment oscillated between highs of $1.0 \times 10^{6}$ to lows of 250,00 recruits in the semi-log mortality model and less so in the logistic mortality model.
(a)
(b)


Results of stock recruitment simulations using semi-log marine mortality for fixed escapement (2.4 eggs $\mathrm{m}^{2}$ ) (a) and fixed exploitation (0.10) (b) policies.


Stock recruitment simulation results derived using logistic marine mortality for (a) fixed escapernent 2.4 eggs $\mathrm{m}^{-2}$ and (b) fixed exploitation of ( 0.10 ) policies.

## Conclusions

The data and analysis of change in size of wild age 2.1 recruits to LaHave River suggests that size selective mortality occurs in the late (month four or greater) marine stage of Atlantic salmon. Years with higher marine mortality are associated with increased robustness and skewed length distributions. Change in size-at-age of recruits may just as well be explained by annual variation in growth or survival of larger faster growing fish in an age class. However, it is difficult to accept that increased growth is associated with lower survival.

The mechanism for non-linear marine survival may be predator attraction and prey switching. Predators only switch to prey species when the prey are abundant enough to satisfy the bioenergetics rules. Marine survival was approximately 0.5 at $2.5 \times 10^{6}$ smolts in the 5.0 maximum smolt production scenario and did not vary greatly in other scenarios (Figure 9). Survival declined to about 0.2 at $5.0 \times 10^{6}$ smolts and to 0.1 at $10 \times 10^{6}$ smolts. This rate of change in survival understandably results in a large change in the number of recruits. This analysis suggests that the maximum rate of change in mortality occurred in the range of $5.0 \times 10^{6}$ to $10.0 \times 10^{6}$ smolts. This range is low relative to the maximum potential smolt production of $55.0 \times 10^{6}$ smolts or relative to the 1996 estimate of $23.0 \times 10^{6}$ smolts (Table 4).

Salmon stocks in pre-settlement time would have been subject to marine predator attraction and freshwater predator attraction. Adult salmon in freshwater would have been particularly vulnerable to predators and have undergone the effects of predators even at low population sizes. Human settlement has done much to reduce the diversity and numbers of natural freshwater predators of salmon. Until the establishment of the Fisheries Act in Canada in 1867, human predators replaced natural predators in the estuaries and rivers. With the loss of habitat and declines of salmon, more restrictive access to the salmon stocks was legislated. By 1984 most of the fishing mortality was removed, and by 1992 fishing mortality was reduced to low levels. Regulations were also evoked that lessened the impact on egg depositions. (This is why a river exploitation of 0.10 was used in the stock recruitment simulations.) The result of these measures was to reduce the variation and increase the numbers of smolts migrating to sea. In effect the mechanisms of predator attraction and prey switching have been dampened. Reductions in secondary production in the North Atlantic, affecting growth and possibly natural mortality, would only serve to exacerbate this situation. The dynamic result is high variation in recruitment.

The measures taken to date in salmon management may well ensure the persistence of the macro-stock but are likely to weigh heavily on small stocks caught up in high marine mortality. If the objective of fisheries management is for high probability of persistence of the macro-stock and large sub-stocks, then this policy is working. An artifact of this policy is high variation in recruitment and reduced probability of recruitment to low freshwater productivity stocks. If the objective of fisheries management is to provide stable fisheries, including in-river fisheries, then the current policy did not, and will not, work.

It would seem that we have unknowingly conducted a rather large-scale Adaptive Management experiment with Atlantic salmon. It has been complicated by concurrent changes in the marine ecosystem, and it is difficult to unravel significant mechanisms. Evaluation of the approach presented here would benefit from extension back to periods earlier in the century when many of the perceived complications of recent years were at least, undetermined.

Fixed exploitation (policy) has been advocated by previous authors (Walters and Parma, 1996). The risk to conservation posed by fixed exploitation policy has been deemed unacceptable by some. It appears there are benefits (more stable recruitment) associated with fixed exploitation policy over fixed escapement policy especially if fish in excess of the spawning requirements are not harvested. The evaluation of threshold rules, as suggested by FAO (Anon.1997), for fixed exploitation policies is a research need in Atlantic salmon management if the trade-off in risk between persistence and yield is to be resolved.

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Table 1. Densities ( $\mathrm{m}^{-2} \times 100$ ) of Atlantic salmon parr determined by electrofishing 13-15 sites in the Miramichi River, 1971-1997, and indices of pre-smolts.

| Year | Parr |  | Pre-smolt index |
| :---: | :---: | :---: | :---: |
|  | Large |  |  |
|  | $(\geq 10 \mathrm{~cm})$ | (<10cm) |  |
| 1971 | 2.3 | 8.6 | 6.7 |
| 1972 | 4.2 | 9.2 | 12.2 |
| 1973 | 1.2 | 3.6 | 1.5 |
| 1974 | 3.3 | 9.4 | 10.9 |
| 1975 | 1.8 | 14.6 | 12.4 |
| 1976 | 4.0 | 13.4 | 13.2 |
| 1977 | 4.2 | 9.4 | 9.3 |
| 1978 | 4.4 | 10.5 | 12.1 |
| 1979 | 2.8 | 8.8 | 9.7 |
| 1980 | 1.9 | 9.4 | 8.4 |
| 1981 | 2.8 | 8.1 | 7.4 |
| 1982 | 3.6 | 10.7 | 11.0 |
| 1983 | 3.2 | 6.2 | 7.9 |
| 1984 | 1.5 | 6.0 | 6.8 |
| 1985 | 0.7 | 8.1 | 5.2 |
| 1986 | 3.6 | 13.5 | 14.6 |
| 1987 | 2.5 | 14.4 | 15.3 |
| 1988 | 1.5 | 10.4 | 9.6 |
| 1989 | 2.4 | 18.2 | 18.2 |
| 1990 | 2.4 | 13.2 | 12.1 |
| 1991 | 3.5 | 17.5 | 16.4 |
| 1992 | 4.6 | 21.8 | 26.0 |
| 1993 | 0.5 | 18.0 | 13.6 |
| 1994 | 4.8 | 23.9 | 22.3 |
| 1995 | 6.4 | 35.1 | 35.1 |
| 1996 | 6.3 | 18.9 | 19.5 |
| 1997 | 5.8 | 32.6 | 33.6 |
| 1998 | 4.7 | mean) |  |

Table 2. Returns of one-sea-winter Atlantic salmon to the southern Gulf of St. Lawrence and to North America, 1971-1996. Proportion southern Gulf of St. Lawrence is of North American total return of one-seawinter fish and proportions Miramichi River return is of total North American return of one-sea-winter fish Estimates were based on Miramichi being 0.5046 of the Gulf of St. Lawrence juvenile salmon production

|  | One-sea-winter total returns |  |  | Proportions |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  | to Gulf of St. Lawrence |  | (NA) North American total rns | 1SW Gulf Miramich of NA of NA return return |  |
|  | min | max |  |  |  |
| 1971 | 33188 | 57918 | 316561 | 0.144 | 0.073 |
| 1972 | 42202 | 73599 | 299913 | 0.193 | 0.097 |
| 1973 | 43681 | 76661 | 321809 | 0.187 | 0.094 |
| 1974 | 65673 | 113924 | 327429 | 0.274 | 0.138 |
| 1975 | 58613 | 101791 | 415247 | 0.193 | 0.097 |
| 1976 | 90307 | 155434 | 443056 | 0.277 | 0.140 |
| 1977 | 31322 | 55905 | 338109 | 0.129 | 0.065 |
| 1978 | 26008 | 45347 | 246468 | 0.145 | 0.073 |
| 1979 | 50872 | 91758 | 338739 | 0.211 | 0.106 |
| 1980 | 45715 | 81291 | 442901 | 0.143 | 0.072 |
| 1981 | 70214 | 126193 | 541583 | 0.181 | 0.091 |
| 1982 | 79858 | 141657 | 457004 | 0.242 | 0.122 |
| 1983 | 25335 | 43737 | 286893 | 0.120 | 0.061 |
| 1984 | 37694 | 63546 | 322155 | 0.157 | 0.079 |
| 1985 | 61244 | 109879 | 374392 | 0.229 | 0.115 |
| 1986 | 114665 | 203466 | 491380 | 0.324 | 0.163 |
| 1987 | 86457 | 154660 | 477253 | 0.253 | 0.127 |
| 1988 | 123433 | 221220 | 539711 | 0.319 | 0.161 |
| 1989 | 72906 | 128831 | 322714 | 0.313 | 0.158 |
| 1990 | 83498 | 155978 | 383135 | 0.313 | 0.158 |
| 1991 | 59574 | 111005 | 260203 | 0.328 | 0.165 |
| 1992 | 146364 | 229318 | 464413 | 0.404 | 0.204 |
| 1993 | 89814 | 144378 | 419311 | 0.279 | 0.141 |
| 1994 | 55623 | 116881 | 306062 | 0.282 | 0.142 |
| 1995 | 26010 | 96239 | 316129 | 0.193 | 0.098 |
| 1996 | 49955 | 97137 | 454203 | 0.162 | 0.082 |
| 1997 |  |  |  | \%. |  |
| Miramichi is: | Gulf NS+ |  | Miramichi is | 0.231 | 0.116 |
|  |  |  | Standard de | 0.076 | 0.038 |
|  | Maximum smolt/unit T |  |  |  |  |
| Miramichi area ( $100 \mathrm{~m}^{2}$ units $)=$ | 546,000 | 33線 1, |  |  |  |

Table 3. Miramichi pre-smolt indices yielding estimates of total North American wild Atlantic salmon smolts in year $i$ at a maximum of $3.5 \mathrm{smolts} \mathrm{m}^{-2} \times 100$ for the maximum per-smolt index; total returns to North American home waters of one sea winter in year $i+1$ and muti-sea-winter in year $i+2$, estimates of pre-fishery abundance in year $i+1$ and $i+2$ with resulting recruitment rate and natural mortality; catches of one-sea-winter in year $i+1$ and two-sea-winter in year i+2 salmon in Salmon Fishing Areas 1-7 and 11 b and $18-14$ with resulting recruitment and natural mortality rates. Table number in ICES 1997/Assess: 10 document is indicated


95 and 96 based on mean proportion Mir.of NA

Table 4. Estimates of the total number of North American smolts produced using Miramichi pre-smolt indices and 2.0 to 5.0 maximum smolts $\mathrm{m}^{-2} * 100$. Mortalities ( M ) are those obtained by

| Year | $\begin{array}{r} \hline \text { Smit } \\ 2 \\ \hline \end{array}$ | $M$ 2 | $\begin{array}{r} \hline \text { Smit } \\ 2.5 \\ \hline \end{array}$ | $M$ 2.5 | Smlt 3 | $M$ 3 | Smlt | $M$ 3.5 | Smit 4 | $M$ 4 | SmH 4.5 | $M$ 4.5 | Smit | $M$ 5 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 72 | 2,215,102 | 0.376 | 2768878 | 0.501 | 3322653 | 0.584 | 3876429 | 0.644 | 4430204 | 0.688 | 4.5 | 4.5 | 5 |  |
| 73 | 2,748,085 | 0.519 | 3435106 | 0.615 | 4122128 | 0.679 | 4809149 | 0.644 0.725 | 4430204 5496170 | 0.688 0.759 | 4983980 | 0.723 | 5537755 | 0.750 |
| 74 | 465,174 |  | 581467 |  | 697761 |  | +814054 | 0.725 | 5496170 930348 | 0.759 | 6183192 | 0.786 | 6870213 | 0.807 |
| 75 | 2,425,149 | 0.411 | 3031436 | 0.528 | 3637723 | 0.607 | 4244010 | 0.663 | 4850297 | 0.705 | 5456584 | 0.738 | 6062872 | 0.764 |
| 76 | 5,934,300 | 0.810 | 7417875 | 0.848 | 8901450 | 0.873 | 10385025 | 0.891 | 11868600 | 0.905 | 13352175 | 0.915 | 14835750 | 0.764 0.924 |
| 77 | 5,607,304 | 0.879 | 7009129 | 0.903 | 8410955 | 0.919 | 9812781 | 0.931 | 11214607 | 0.940 | 12616433 | 0.946 | 14018259 | 0.952 |
| 78 | 2,716,599 | 0.542 | 3395749 | 0.634 | 4074899 | 0.695 | 4754049 | 0.738 | 5433198 | 0.771 | 6112348 | 0.796 | 6791498 | 0.817 |
| 79 | 5,195,602 | 0.733 | 6494503 | 0.787 | 7793403 | 0.822 | 9092304 | 0.848 | 10391205 | 0.867 | 11690105 | 0.881 | 12989006 | 0.893 |
| 80 | 3,307,021 | 0.571 | 4133776 | 0.657 | 4960532 | 0.714 | 5787287 | 0.755 | 6614042 | 0.786 | 7440798 | 0.810 | 8267553 | 0.829 |
| 81 | 2,143,796 | 0.441 | 2679745 | 0.553 | 3215694 | 0.627 | 3751643 | 0.681 | 4287592 | 0.720 | 4823541 | 0.752 | 5359490 | 0.776 |
| 82 | $3,770,129$ $4,322,735$ | 0.803 0.827 | 4712662 | 0.842 | 5655194 | 0.868 | 6597726 | 0.887 | 7540259 | 0.901 | 8482791 | 0.912 | 9425323 | 0.921 |
| 84 | 4,12,785 $\mathbf{2 , 1 2 0 , 6 8 5}$ | 0.827 0.506 | 5403419 2650857 | 0.861 0.605 | 6484103 3181028 | 0.884 0.671 | 7564787 | 0.901 | 8645471 | 0.913 | 9726155 | 0.923 | 10806838 | 0.931 |
| 85 | 1,287,815 | 0.023 | 1609769 | 0.219 | 1931723 | 0.349 | 2253677 | 0.718 0.442 | 4241371 | 0.753 | 4771542 | 0.781 | 5301713 | 0.803 |
| 86 | 1,276,340 | 0.034 | 1595426 | 0.227 | 1914511 | 0.356 | 2233596 | 0.448 | 2552681 | 0.517 | 2897584 | 0.566 | 3219538 | 0.609 |
| 87 | 2,825,121 | 0.600 | 3531401 | 0.680 | 4237681 | 0.734 | 4943962 | 0.772 | 5650242 | 0.800 | 6356522 | 0.822 | 3190851 | 0.613 |
| 88 | 3,017,362 | 0.736 | 3771703 | 0.789 | 4526044 | 0.824 | 5280384 | 0.849 | 6034725 | 0.868 | 6789065 | 0.883 | 7543406 | 0.840 0.894 |
| 89 | 1,887,539 | 0.602 | 2359424 | 0.681 | 2831308 | 0.734 | 3303193 | 0.772 | 3775078 | 0.801 | 4246963 | 0.823 | 4718847 | 0.894 0.841 |
| 90 | 3,414,517 | 0.809 | 4268146 | 0.847 | 5121776 | 0.872 | 5975405 | 0.891 | 6829034 | 0.904 | 7682663 | 0.915 | 8536293 | 0.841 0.923 |
| 91 | 1,846,279 | 0.650 | 2307849 | 0.720 | 2769419 | 0.767 | 3230988 | 0.800 | 3692558 | 0.825 | 4154128 | 0.844 | 4615698 | 0.860 |
| 92 | 3,624,909 | 0.847 | 4531136 | 0.878 | 5437363 | 0.898 | 6343591 | 0.913 | 7249818 | 0.924 | 8156045 | 0.932 | 9062272 | 0.939 |
| 93 | 5,676,451 | 0.921 | 7095563 | 0.937 | 8514676 | 0.948 | 9933789 | 0.955 | 11352901 | 0.961 | 12772014 | 0.965 | 14191126 | 0.969 |
| 94 | 4,344,411 | 0.896 | 5430514 10599505 | 0.917 | 6516617 | 0.931 | 7602720 | 0.940 | 8688823 | 0.948 | 9774925 | 0.954 | 10861028 | 0.958 |
| 95 | $8,479,604$ $9,385,020$ | 0.944 | 10599505 | 0.955 | 12719406 | 0.963 | 14839306 | 0.968 | 16959207 | 0.972 | 19079108 | 0.975 | 21199009 | 0.978 |
| 96 97 | $9,385,020$ $5,501,020$ |  | 11731275 6876275 |  | 14077530 8251530 |  | 16423785 |  | 18770040 |  | 21116295 |  | 23462550 |  |
|  | 5,501,020 |  | 6876275 |  | 8251530 |  | 9626785 |  | 11002040 |  | 12377295 |  | 13752551 |  |

Table 5. Forecast simulations of 1 SW and 2SW recruits of North American Atlantic salmon derived from regressions of Recruits on the logarithm of total NA Smolt index, Habitat index, and Year. Smolt index was derived from Miramichi Pre-smolt index at 5.0 smolts $\mathrm{m}^{-2} \times 100$ maximum production and proportion Miramichi is of the total 1 SW return. Simulations were run using the mean and standard error of the Miramichi proportion ( $0.116_{ \pm} 0.038$ ) and forecast values and standard error of the forecast values of habitat variables that will contribute to those returns.

| $\begin{gathered} \text { Return } \\ \text { year } \\ \hline \end{gathered}$ | Pre_smolt | HabFEB | Std_err_est | Simulation Estimates |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  | Mean | Mode | 5 5treercentile | 95inPercentile |
|  |  |  |  |  |  |  |  |
| 1997 | 35.1268 | 1594 | - | 441,870 | 454,562 | 379,213 | 485,888 |
| 1998 | 19.4656 | 1722 | 124.205 | 563,443 | 522,807 | 425,206 | 701,457 |
|  |  |  |  |  |  |  |  |
| 1997 | 22.3 | 1419 | - | 62,680 | 75,511 | 51 | 105,890 |
| 1998 | 35.1 | 1605 | - | 59,732 | 76,073 | 0 | 103,756 |
| 1999 | 19.5 | 1587 | 137.399 | 89,790 | 105,294 | 0 | 168,900 |
| Deterministic forecasts for 2SW returns |  |  |  |  |  |  |  |
| 1997 |  |  |  | 37,012 |  | 0 | 136,091 |
| 1998 |  |  |  | 65,926 |  | 0 | 171,546 |
| 1999 |  |  |  | 90,215 |  | 0 | 193,055 |

Table 6. Summary statistics and coefficient of skewness for lengths of wild age 2.1
Atlantic salmon sampled at Morgan Falls, LaHave River, Nova Scotia, 1970 to 1997.

|  | Fork length (cm) |  |  |  |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  |  |  | Coefficient <br> of |  |  |
| Year | N | Mean | Mode | Min | Max | deviation | Skewness |  |
| 1970 | 3 | 55.67 |  | 54.60 | 56.50 | 0.97 | -1.019 |  |
| 1973 | 9 | 54.48 |  | 50.80 | 57.40 | 2.37 | -0.211 |  |
| 1974 | 7 | 57.03 |  | 53.00 | 60.70 | 3.22 | 0.107 |  |
| 1975 | 4 | 56.43 |  | 54.60 | 58.50 | 1.83 | 0.210 |  |
| 1976 | 51 | 54.37 | 55.50 | 50.40 | 58.20 | 1.75 | -0.006 |  |
| 1977 | 58 | 53.36 | 54.00 | 43.50 | 58.50 | 3.08 | -0.968 |  |
| 1978 | 24 | 52.76 | 53.80 | 48.20 | 58.80 | 2.26 | 0.151 |  |
| 1979 | 116 | 52.40 | 52.50 | 45.50 | 57.60 | 2.32 | -0.028 |  |
| 1980 | 139 | 54.04 | 53.40 | 46.90 | 60.70 | 2.42 | 0.415 |  |
| 1981 | 148 | 54.58 | 57.00 | 48.00 | 63.20 | 2.75 | 0.267 |  |
| 1982 | 116 | 54.57 | 54.20 | 48.60 | 63.20 | 2.67 | 0.350 |  |
| 1983 | 185 | 53.80 | 54.00 | 47.60 | 60.70 | 2.27 | 0.153 |  |
| 1984 | 216 | 54.14 | 55.40 | 47.00 | 61.50 | 2.89 | -0.153 |  |
| 1985 | 187 | 53.11 | 53.00 | 45.00 | 63.00 | 2.92 | 0.077 |  |
| 1986 | 188 | 55.87 | 56.00 | 5.00 | 63.00 | 2.71 | 0.140 |  |
| 1987 | 457 | 54.86 | 54.20 | 48.60 | 63.50 | 2.47 | 0.629 |  |
| 1988 | 596 | 54.59 | 54.20 | 45.00 | 66.50 | 2.52 | 0.049 |  |
| 1989 | 634 | 53.99 | 53.20 | 48.20 | 63.60 | 2.43 | 0.333 |  |
| 1990 | 592 | 54.69 | 55.50 | 47.10 | 64.00 | 3.03 | 0.408 |  |
| 1991 | 162 | 53.86 | 53.70 | 47.70 | 61.50 | 2.43 | 0.256 |  |
| 1992 | 775 | 53.98 | 53.00 | 47.10 | 63.00 | 2.57 | 0.397 |  |
| 1993 | 258 | 53.67 | 53.50 | 47.70 | 64.30 | 2.59 | 0.704 |  |
| 1994 | 130 | 55.21 | 55.30 | 48.10 | 64.70 | 3.30 | 0.729 |  |
| 1995 | 133 | 53.22 | 54.50 | 48.00 | 59.00 | 2.27 | 0.205 |  |
| 1996 | 140 | 54.98 | 53.00 | 50.00 | 62.00 | 2.35 | 0.290 |  |
| 1997 | 124 | 55.21 | 56.50 | 49.60 | 60.50 | 2.43 | 0.139 |  |
|  |  |  |  |  |  |  |  |  |

North American Total Returns of Atlantic salmon to Homewaters and to Spawning Escapement


Figure 1. Returns and spawning escapement to North America 1971 to 1996.

Miramichi Pre-smolt Index


Figure 2. Miramichi river pre-smolt indices 1971 to 1997.

Miramichi returns as proportion of the North American stock (returns+harvests)


Figure 3. Atlantic salmon returns to the Miramichi River as a proportion of the total North American stock.


Figure 4. Portion of the variance in North American smolt estimates accounted for in the Miramichi River pre-smolt index.

Total N.A. Smolts calibrated using maximum production rates of 2.0-5.0 smolt $/ 100 \mathrm{~m}^{2}$ and Miramichipre-smolt indices


Figure 5. Estimates of the annual number of wild smolts as indexed by the Miramichi pre-smolt density at maximum smolt production rates of 2.0 to 5.0 smolts $\mathrm{m}^{-2} \mathbf{x} 100$.

Pre-fisheries vs NA Smolt


Figure 6. Estimated number of North American smolts compared to the pre-fishery estimate of North American salmon.


Figure 7. Estimated smolt production and recruitment rate of North American Atlantic salmon, 1972 to 1997.

Mortality of N.A.smolts at maximum production rates of 2.0 - 5.0 smolt $/ 100 \mathrm{~m} 2$ and Miramichi pre-smolt indicies


Figure 8. Sensitivity of mortality estimates to values of maximum smolt production rates.

Natural mortality of North American smolt estimates made at maximums of 2.0-5.0 smolt / $100 \mathrm{~m}^{2}$ and Miramichi pre-smolt indicies


Figure 9. Marine mortality curves for maximum smolt production rates of 2.0 to 5.0 smolts $\mathrm{m}^{-\mathbf{2}} \mathbf{x} 100$.

Residuals Observed-Expected Total Recruits


Figure 10. Residuals from the product of annual estimates of North American Atlantic salmon smolt production and annual estimates of mortality,
differenced with the observed total recruits to all fisheries and ress differenced with the observed total recruits to all fisheries and returns to homewaters.

## Residuals of Salmon Recruit Model on Marine Habitat



Figure 11. Scatter plot of residuals, numbers of Atlantic salmon recruits, from the product of estimated mortality times smolt estimates and differenced from the observed total recruits, plotted with marine habitat indices in year $i+1$ of the smolt year.

## Residuals of Salmon Recruit Model on Marine Habitat



Figure 12. Scatter plot of residuals, numbers of Atlantic salmon recruits, from the product of estimated mortality times smolt estimates and differenced from the observed total recruits, plotted with marine habitat indices in year $\mathbf{i}+2$ of the smolt year.


Figure 13. North American Atlantic salmon run size forecast cross-validation (leave-one-out) for 1SW recruits (1979-95). Diagonal line is the $\mathbf{1 : 1}$ line. Vertical lines are $\mathbf{9 0 \%}$ prediction intervals.

## MSW



Figure 14. North American Atlantic salmon run size forecast cross-validation (leave-one-out) for MSW recruits (1972-94). Diagonal line is the $1: 1$ line. Vertical lines are $90 \%$ prediction intervals.

Mean length wild age 2.1 at Morgan Falls vs. year of return


Figure 15. Mean length of age 2.1 Atlantic salmon returning to Morgan Falls on the LaHave River. Standard deviation of the mean is shown in the vertical bars.

| Two step stock recruit model: |
| :--- |
| Smolt production is modeled by a |
| Beverton-Holt model and smolts |
| are exposed to semi-log mortality. |
|  |
|  |


| Bev-Holt | $\mathrm{R}=\mathrm{a}^{*} \mathrm{~S} / 1+\left(\mathrm{a}^{1 / 2} \mathrm{~b}^{\prime \prime}\right)^{*} \mathrm{~S}$ |
| :---: | :---: |
| a | b |
| \% | 35xemefee |
| $\begin{aligned} & \mathbf{a}^{\prime}=\text { initial } \\ & \mathbf{b}^{\prime \prime}=\text { max. } \end{aligned}$ | x smolts/spwner It production |

Smolt mort= A*Lnx-B

A=population@50\% of max. mortality B=slope or rate of increase in mortality C=maximum mortalit(\%)

| Simulation Bounds |  |
| ---: | ---: |
| Smin | Increment |
| Smax | Rmax |
| $\mathbf{S 4 4 , 0 0 0}$ | $16,513,995$ |
| Mmin | Mmax |
| 0.28 | 1.00 |


| Rtn max |
| :--- |
| $1,172,038$ |
| S@Rtn max |
| 272,000 |
| Yield@Rtn max |
| 900,038 |



Figure 16 Two step stock-recruitment relationship derived using a a Beverton - Holt production of smolts and semi-logarithmic survival for smolt to recruit. The model is calibrated to total North American stock of Atlantic salmon.

| Two step stock recruit model: |
| :--- |
| Smolt production is modeled by a |
| Beverton-Holt model and smolts |
| are exposed to logistic mortality. |
|  |
|  |


| Bev-Holt R $\quad$ a ${ }^{*} \mathrm{~S} / 1+\left(a^{1 /} / \mathrm{b}^{\prime \prime}\right) * S$ |  |  |
| :---: | :---: | :---: |
| - b |  |  |
| 20ens imeemeg |  |  |
| $\mathbf{a}^{\prime}$ =initial max smolts/spwner b"=max.smolt production |  |  |
|  |  |  |
| Smolt mort C**Pop^B $^{\text {A }}$ |  |  |
|  |  | $\overline{A^{\wedge} B+P^{\prime} p^{\wedge} B}$ |
| A | B | C |
| 255cedeg | \% 3 \% ${ }^{\text {5 }}$ | 1) |

A=population@50\% of max. mortality $\mathrm{B}=$ slope or rate of increase in mortality
C=maximum mortalit(\%)

| Simulation Bounds |  |
| :---: | :---: |
| Smin | Increment |
| Kmax | 15M68 |
| Smax | Rmax |
| 944,000 | 14,055,225 |
| Mmin | Mmax |
| 0.00 | 97:80 |


| Rtn max |
| :--- |
| $1,287,896$ |
| S@Rtn max |
| 112,000 |
| Yield@Rtn_max |
| $1,175,896$ |



Figure 17. Two step stock-recruitment relationship derived using a a Beverton - Holt production of smolts and logistic survival for smolt to recruit. The model is calibrated to total North American stock of Atlantic salmon.


Figure i. Plot of cumulative mortality of Atlantic salmon by month (Doubleday et al. 1979)


Figure ii. Effect of varying the slope parameter in the mortality function.


[^0]:    ${ }^{1}$ D. G. Reddin, Department of Fisheries and Oceans, Newfoundland Region, P.O. Box 5667, St. John's, Newfoundland, Canada A1C 5X1

[^1]:    ${ }^{2}$ Systat 7.0 for Windows. Chicago, II. SPSS Inc. 1997.

[^2]:    Durbin-Watson D Statistic $\quad 1.614$
    First Order Autocorrelation 0.152

