



Fisheries and Oceans Pêches et Océans
Canada Canada

Canadian Stock Assessment Secretariat
Research Document 98/84

Secrétariat canadien pour l'évaluation des stocks
Document de recherche 98/84

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**The abundance of Harp seals in the North Atlantic and recruitment of the North American
stock of Atlantic salmon (*Salmo salar*)**

by

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ISSN 1480-4883

Ottawa, 1998

Canada

Abstract

The negative trend in marine survival of North American (NA) Atlantic salmon (*Salmo salar*) has persisted in spite of severely reduced commercial salmon fisheries. This document explores the potential of replacing YEAR, a simple metric vector that accounted for a significant proportion of the variation in recruitment of salmon, with annual population estimates of harp seals (*Phoca groenlandica*). Harp seals were investigated as a replacement for YEAR because of their increasing population and their estimated consumption of salmon in the Northern Gulf of St. Lawrence. In 1996, the consumption of salmon may have exceeded 3.0×10^6 salmon in the Northern Gulf of St. Lawrence. Harp seals are estimated to have consumed 82% of the total seal consumption of fish in 1996 and are coincident with NA salmon for extended periods. The population of harp seals, interaction with the marine habitat area of salmon and an index of annual NA smolt production accounted for 0.94 of the variation in recruitment of NA multi-sea-winter salmon for the period 1973 to 1995. Similar models accounted for 0.86 of the recruitment of NA one-sea-winter salmon for the period 1979 to 1996. Models using seal abundance rather than YEAR provide an ability to forecast trends and more importantly, because the variable is not a simple vector, turning points in the annual recruitment of salmon. Recruits of the 1977 smolt year were outliers to the models and did not follow a pattern of increased size of one-sea-winter salmon. Factors other than predation are suggested for the reduced marine survival of the 1977 smolt class.

Résumé

La tendance négative de la survie en mer du saumon atlantique (*Salmo salar*) de l'Amérique du Nord (NA) s'est maintenue en dépit de pêches commerciales du saumon très sévèrement réduites. Le document examine la possibilité de remplacer YEAR, un vecteur métrique simple, qui expliquait une partie appréciable de la variation du recrutement du saumon, par des estimations de population annuelles du phoque du Groenland (*Phoca groenlandica*). L'examen a porté sur le phoque du Groenland à cause de l'augmentation de sa population et de sa consommation estimée de saumons dans la partie nord du golfe du Saint-Laurent. En 1996, cette consommation a pu dépasser $3,0 \times 10^6$ saumons dans la partie nord du Golfe. On estime que le phoque du Groenland a consommé 82 % de tout le poisson consommé par les phoques en 1996 et que cette espèce se rencontre au même endroit que le saumon nord-américain pendant de longues périodes. La population de phoque du Groenland, les interactions avec l'habitat marin du saumon et un indice de la production annuelle de saumoneaux NA expliquaient 0,94 de la variation du recrutement du saumon NA pluribermarin pendant la période 1973-1995. Des modèles semblables permettaient d'expliquer 0,86 du recrutement des saumons unibermarins pendant la période 1979-1996. Les modèles fondés sur l'abondance des phoques plutôt que sur le paramètre YEAR permettent de prévoir les tendances et, ce qui est plus important, cette variable n'étant pas un vecteur simple, les points d'inflexion du recrutement annuel du saumon. Les valeurs de recrutement des saumoneaux de l'année 1977 étaient des valeurs aberrantes des modèles et ne présentaient pas l'allure de l'augmentation de taille des saumons unibermarins. Des facteurs autres que la prédation sont proposés pour expliquer le faible taux de survie en mer de la classe des saumoneaux de 1977.

Introduction

A high proportion ($R^2 = 0.63$) in the variation in total recruitment of the North American stock of non-maturing one-sea-winter (1SW) Atlantic salmon has been explained by indices of Atlantic salmon marine habitat area (Reddin and Friedland 1993). This pre-fishery abundance model was improved ($R^2 = 0.71$) with the addition of a parental stock variable which, in order to remain significant, excluded estimates of parental stock from the United States and from the Gulf of St. Lawrence portion of Canada (Anon 1997).

Habitat indices for the months January, February, March and April were found by Reddin and Friedland (1993) to best account for variance in pre-fishery abundance of North American salmon in the North Atlantic Ocean. Models presented by Amiro (MS1998), which included indices of North American smolt production and marine habitat area for salmon provided estimates for both 1SW and MSW North American salmon recruitment. The addition of the smolt index variable increased the proportion of the explained variance by 13% for 1SW salmon recruits and 15% for 2SW recruits from models using only recruits and winter habitat. The addition of a simple metric vector (YEAR) further increased the accounted variance by 0.05 for one-sea-winter recruits for the period 1979 to 1996 and 0.14 for multi-sea-winter recruits for the period 1972 to 1995. The addition of YEAR in the model for multi-sea-winter recruits for the period 1972 to 1995 without including 1977 further increased the explained variance by 0.22 for a total explained variance of 0.94. YEAR accounted for the monotonic decrease in recruitment rate of North American origin Atlantic salmon. While YEAR can account for some of the explained variance in an empirical model for a specific time period with a monotonic trend, it cannot be used in any reasonable theoretical model for recruitment of North American origin Atlantic salmon. The desire to replace the YEAR variable in these models with a biologically meaningful variable was suggested.

The positive skewed distribution of fork lengths in a single age class and run time of salmon measured at Morgan Falls on the LaHave River, Nova Scotia, could indicate that selective removal of smaller fish-at-age had occurred. Positive skewness in the distribution of fork lengths of age 2.1 salmon measured at Morgan Falls showed a significant ($p = 0.007$) increase during the period 1985 to 1997 (Fig. 1.), (Amiro *et al.* MS 1998). Evidence of selective removal of the smaller sizes of age 2.1 (freshwater winters.seawinters) salmon returning before August to Morgan Falls fishway on the LaHave River was observed in 1997 and in earlier years. In addition to the increase in skewness, selection was also suggested by consistent larger size and condition of age 2.1 salmon measured at the fishway in 1997 (Fig. 2). The average fork length of one-sea-winter salmon was also longer for the returns to the Miramichi River in 1997 (Chaput *et al.* MS 1998). These data suggest that selective fishing for larger fish did not occur in 1997 when commercial fisheries in the northwest Atlantic were limited and reported only 27,947 one-sea-winter fish harvested. Had the commercial fishery been selectively removing larger fish prior to 1984, when the fisheries were reduced, then a return to a normal distribution from a negatively skewed distribution would have been expected after the close of the fisheries. Instead, a positive skewness in fish size was observed. These data suggest selective removal or survival of fish based on size in the 1984 to 1997 time period. This paper examines the prospect of selective removal by predation to account for the change in size distribution and reduced recruitment. This analysis postulates that reduced recruitment is the result of an increased predator population and interaction with the environment of the North Atlantic Ocean.

A potential predator of salmon in the North Atlantic that has substantially increased in population during the downturn in recruitment of Atlantic salmon is seals. Hammill and Stenson (1997) indicate that four species of seals are common throughout Atlantic Canada. Gray seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) are abundant along the coast from the northeastern United States to Hamilton Inlet and in the Gulf of St. Lawrence. Harp seals (*Phoca groenlandica*) and hooded seals (*Cystophora cristata*) are seasonal residents. They estimated

that seals consumed 3.4 million tons of prey (mostly fish) in Atlantic Canada in 1996 and harp seals accounted for 82% of this consumption. Gray seals accounted for 7% and hooded seals 10%. The reported primary size range of cod consumed by harp seals is 10-20 cm (Lawson and Stenson 1995). However, the incidence of cod >40cm ranged from 1.3 to 17.6% in the Northern Gulf of St. Lawrence and in areas 2J3KL Northern Newfoundland and Southern Labrador coast (Hammill and Stenson, Table 3, 1997).

The estimated consumption of salmon by seals, mostly in the Northern Gulf of St. Lawrence, has increased from 2,281 t in 1990 to 3,015 t in 1996 (Hammill and Stenson 1997). At 1.0 kg salmon⁻¹ (an approximate weight of a 40 cm salmon) this is the equivalent of 3.0×10^6 salmon. There are, however, several problems associated with this estimate: 1) The estimate is based on only one observation of a salmon in the stomach of a harp seal in an estuary area of the northern Gulf of St. Lawrence. 2) While there is theoretic reason (Friedland *et al.* 1999) to suspect salmon post-smolts are in the Gulf of St. Lawrence during the harp seal residence period (December to May) there is little direct observation of post-smolts recorded in this area. 3) The estimate assumes that the diet of harp seals in coastal Newfoundland and offshore is the same as that of the northern Gulf of St. Lawrence.

The Gulf of St. Lawrence is estimated to hold 25% of the population of harp seals during the December to May period. Following whelping female harp seals undergo a short feeding period before hauling out on the pack ice to molt. Once the molt is complete the animals remain in southern waters until late spring or early summer before returning to the Arctic for the later summer and autumn. There is some indication that seals may move between the Gulf and Front whelping patches (Stenson *et al.* 1995a). The estimated consumption of salmon by seals in NAFO area 2J3KL and the Flemish Cap in any year from 1990 to 1996 was 0. The 2J3KL area was estimated to contain 29% of the adult population of adult harp seals.

The lack of salmon in the stomach contents of seals sampled in 2J3KL and the Flemish Cap may not be accepted as evidence of the complete lack of salmon in the diet of seals in these areas. Without knowing the numbers, distribution and conditions under which samples were obtained a zero incidence cannot be interpreted as an absolute absence of salmon in diet of harp seals in these areas. The population of harp seals in 1996 was estimated to be 4.8×10^6 seals (pers. comm. M.O. Hammill)¹. To obtain an almost certain probability of observing a single salmon in the diet of harp seals in 1996, if all remaining seven month old post-smolts were consumed by harp seals, would require 7,691 samples (Cairns MS1998). Cairns (1998) estimates that at 100% predation of salmon by harp seals, salmon would comprise 0.01% of the total diet of harp seals. The incidence of salmon in the diet of seals in the Northern Gulf area provides some evidence that salmon are at least an occasional component of the diet of adult harp seals. If individual seals develop a preference for salmon then the large population, long life span of harp seals (25+ years, Sjare *et al.* 1996) and the migration pattern of adult seals in the Gulf of St. Lawrence to the front (NAFO area 2J3KL) conditioned to prey on salmon could result in significant consumption of salmon by seals. The spatial coincidence of harp seals and salmon is assured because of their similarities in prey species (Lear 1980, Lawson and Stenson 1995).

Synchrony of recruitment among Atlantic salmon stocks has been previously documented (Scarnecchia *et al.* 1989; Reddin and Shearer 1987; Friedland *et al.* 1993). Because Atlantic salmon originate from a diverse geographic range, Northeastern United States to Ungava Bay, Canada, a common factor acting at a common temporal and spatial location would explain this synchrony. If this common factor is predation then the spatial dimension may be as large as the interaction field of the salmon and the predator. Atlantic salmon of most rivers in North America occupy a common spatial and temporal location during the late winter. This area is the South Labrador sea including coastal Newfoundland (Ritter 1989). Seals also occupy this vast area and prey on similar fish species. An alternate hypothesis to coincident distribution could be that

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there is more than one wintering area for Atlantic salmon and all areas are also occupied by seals.

This document examines the significance of replacing the YEAR variable with annual population estimates of harp seals in recruitment models (Amiro MS1998) of one-sea and multi-sea-winter North American Atlantic salmon. Interaction of the seal population with the index of winter habitat area for salmon is also examined for significant contribution to explanation of the variance in recruitment. Also, this hypothesis explains the positive skewness observed in the size of single age and run-time one-sea-winter returns to Morgan Falls, LaHave River, as well as the general increase in size of one-sea-winter salmon observed at other monitoring facilities.

Methods

Indices of smolt production are those of Amiro (MS1998) and are derived from estimates of pre-smolts determined from estimated mean parr densities 1971 to 1997 in the Miramichi River, New Brunswick. Smolt estimates are derived by scaling up the parr densities to a maximum smolt production value of $5.0 \text{ m}^{-2} \times 100$. Thus maximum parr densities are calibrated to the maximum smolt production rate. Smolt estimates are also annually scaled to the North American production of salmon from the proportion Miramichi was of the annual return of one-sea-winter salmon to all North American rivers (Table 1).

One-sea-winter and multi-sea-winter recruits, were those reported by ICES 1997 (Anon. 1997). The sum of recruits were as reported by Amiro (MS1998) and were factored by dividing by 1000 to bring them into the range of other variables in the models.

Annual indices of habitat area for salmon (**Habitat**) were those of Reddin and Friedland (1993) as reported by Anon. (1997) and D. Reddin (pers. comm.)².

Annual estimates of the numbers of harp seals (**Harp**) in year $i + 1$ of the smolt emmigration year were those of Shelton *et al.* (1996) for the years 1973 to 1994. Estimates for the years 1995 to 1996 were provided by M. Hammill (pers. comm.)¹. Harp seal population were factored by 100,000 (**HARP2**) to conform to the range of other variables in the models.

Models examined were those of Amiro (MS1998) and were of the general form;

Recruits = constant + Ln(smolt index) + Habitat + Harp + (HabitatXHarp) + error

Habitat month February of smolt year $i+1$ was used for one-sea-winter recruits and habitat month March of smolt year $i+1$ was used for multi-sea-winter recruits. The interaction of habitat and harp seals (HabitatxHarp) was tested for significance in the initial model specification. Backward stepwise regression (SYSTAT V5.0) with an F to enter of 0.05 and an F to reject of 0.05 was used to reduce non-significant ($p < 0.05$) variables and thereby select variables for final inclusion in the models.

² D.G. Reddin, Department of Fisheries and Oceans, Newfoundland Region, P.O. Box 5667, St. John's, Newfoundland, Canada A1C 5X1

Results

Multi-sea-winter recruitment:

MODEL_1) Backward stepwise regression rejected the seal population variable (**HARP**) and retained the smolt index (**LNSMOLT_5**), March HabitatxHarp (**HMARXHARP**) interaction and March habitat area (**LHBTMAR**). This model accounted for 0.84 of the variation in MSW recruitment and was highly significant ($p < 0.000001$)

Model_1 : MSW_RECRUITS = Constant + LNSMOLT_5 + HMARXHARP + LHBTMAR

Diagnostics:

Dep Var: MSW_RECRUITS N: 22 Multiple R: 0.92975 Squared multiple R: 0.86443

Adjusted squared multiple R: 0.84183 Standard error of estimate: 7.52929

Effect	Coefficient	Std Error	Std Coef	Tolerance	t	P(2 Tail)
CONSTANT	216.46621	58.82652	0.0	.	3.67974	0.00171
LNSMOLT_5	-14.03621	3.70861	-0.33295	0.97327	-3.78477	0.00136
HMARXHARP	-0.73335	0.17575	-0.38653	0.87777	-4.17278	0.00057
LHBTMAR	4.85493	0.64584	0.70523	0.85576	7.51720	0.00000

Analysis of Variance

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
Regression	6506.33963	3	2168.77988	38.25664	0.00000
Residual	1020.42508	18	56.69028		

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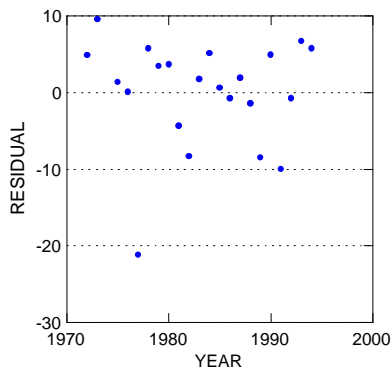
Case 6 is an outlier (Studentized Residual = -4.54543)

Durbin-Watson D Statistic 2.053

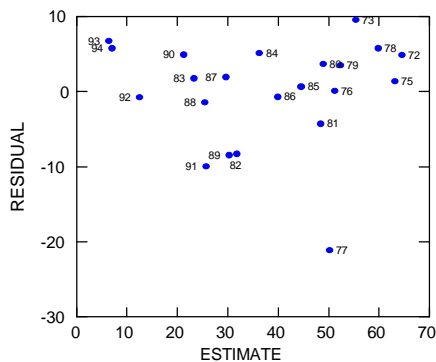
First Order Autocorrelation -0.054

Plots of the residuals including Case 6 (1977) are as follows:

MSW_RECRUITS = CONSTANT+LNSMOLT_5+HMARXHARP+LHBTMAR



MSW_RECRUITS=CONSTANT+LNSMOLT_5+HMARXHARP+LHBTMAR



MODEL_2) In the first model (1) 1977 was a significant outlier. Excluding 1977 the model retained the same variables and accounted for 0.93 of the variation in the recruitment of MSW salmon.

Model_2 : MSW_RECRUITS = Constant + LNSMOLT_5 + HMARXHARP + LHBTMAR

Diagnostics:

Dep Var: MSW_RECRUITS N: 21 Multiple R: 0.96859 Squared multiple R: 0.93817

Adjusted squared multiple R: 0.92726 Standard error of estimate: 5.20529

Effect	Coefficient	Std Error	Std Coef	Tolerance	t	P(2 Tail)
CONSTANT	155.40842	42.83004	0.0	.	3.62849	0.00208
LNSMOLT_5	-10.56865	2.67499	-0.23909	0.99325	-3.95091	0.00103
HMARXHARP	-0.74675	0.12154	-0.39294	0.88933	-6.14422	0.00001
LHBTMAR	5.35289	0.45974	0.74668	0.88443	11.64331	0.00000

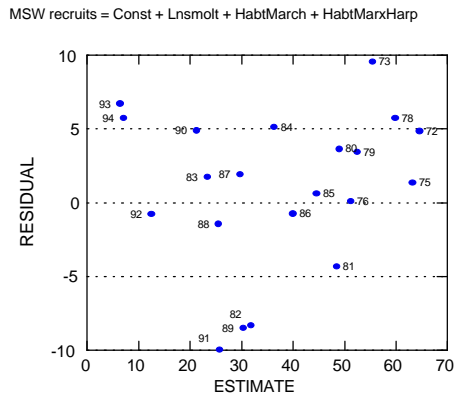
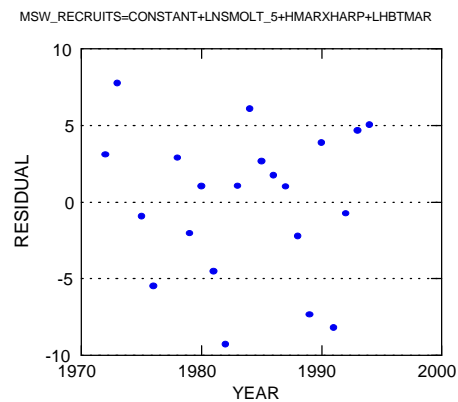
Analysis of Variance

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
Regression	6988.74041	3	2329.58014	85.97796	0.00000
Residual	460.61642	17	27.09508		

Durbin-Watson D Statistic 1.772

First Order Autocorrelation 0.076

Plots of the residuals from model (2) displayed no obvious temporal or scalar trends.



One-sea-winter recruitment

MODEL_3) Backward stepping regression rejected the February habitat variable. The remaining variables accounted for 0.55 of the variation in recruitment of 1SW salmon:

MODEL_3: ISW_RECRUITS = CONSTANT+LNSMOLT_5+HFEBXHARP+HARP2

Diagnostics:

Dep Var: ISW_RECRUITS N: 23 Multiple R: 0.78405 Squared multiple R: 0.61473

Adjusted squared multiple R: 0.55390 Standard error of estimate: 11.78039

Effect	Coefficient	Std Error	Std Coef	Tolerance	t	P(2 Tail)
CONSTANT	298.62340	82.99659	0.0	.		3.59802 0.00192
LNSMOLT_5	-14.67522	5.18705	-0.40789	0.97556	-2.82920	0.01072
HFEBXHARP	1.30367	0.50224	0.84645	0.19068	2.59572	0.01775
HARP2	-2.20768	0.58220	-1.24298	0.18871	-3.79194	0.00123

Analysis of Variance

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
Regression	4207.27988	3	1402.42663	10.10557	0.00034
Residual	2636.77517	19	138.77764		

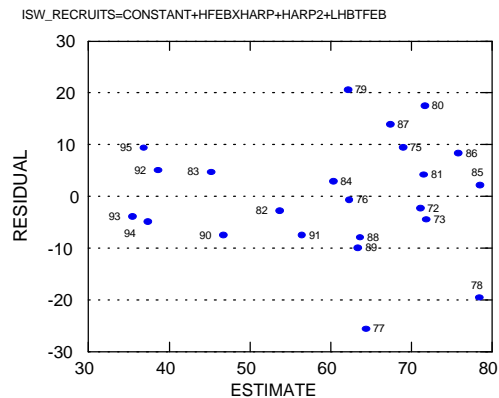
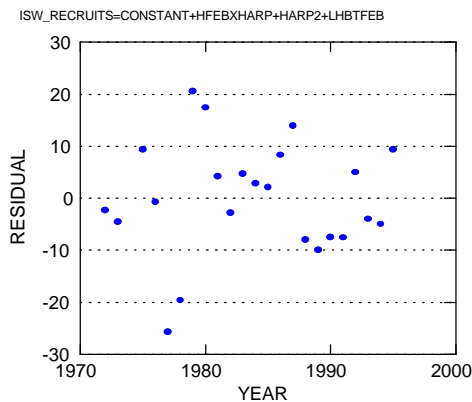
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Case 6 is an outlier (Studentized Residual = -2.85907)

Durbin-Watson D Statistic 1.468

First Order Autocorrelation 0.248

Again the 1977 data point was a significant outlier to the model and the residuals are at the extremes from 1977 to 1980.



MODEL_4) When the the 1977 data was excluded backward stepwise regression rejected the LNSMOLT_5 variable. The resulting model accounted for 0.67 of the variation in one-sea-winter recruitment.

MODEL_4: ISW_RECRUITS = CONSTANT+HFEBXHARP+HARP2+LHBTFFEB

Dep Var: ISW_RECRUITS N: 22 Multiple R: 0.84756 Squared multiple R: 0.71835

Adjusted squared multiple R: 0.67141 Standard error of estimate: 9.98071

Effect	Coefficient	Std Error	Std Coef	Tolerance	t	P(2 Tail)
CONSTANT	212.80818	63.09014	0.0	.	3.37308	0.00339
HFEBXHARP	4.50719	1.29961	3.00715	0.02081	3.46810	0.00274
HARP2	-7.29483	1.98753	-4.15455	0.01221	-3.67030	0.00175
LHBTFFEB	-8.85308	3.85584	-1.20032	0.05725	-2.29602	0.03390

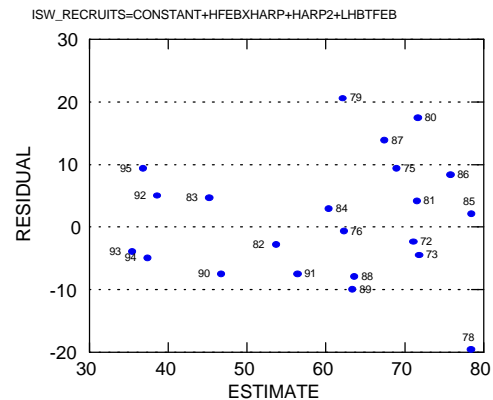
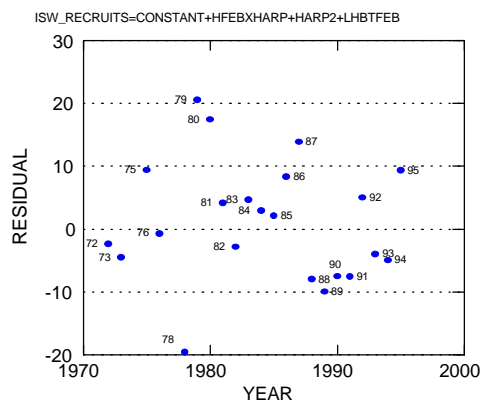
Analysis of Variance

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
Regression	4573.26447	3	1524.42149	15.30319	0.00003
Residual	1793.06321	18	99.61462		

Durbin-Watson D Statistic 1.660

First Order Autocorrelation 0.166

Plots of the residuals shows a negative trend after 1978.



Model_5) The backward stepping model run on the one-sea-winter data for smolt years 1979 to 1995 resulted in a highly significant ($p < 0.000001$) model accounting for 0.86 of the variance in one-sea-winter recruitment.

MODEL_5: ISW_RECRUITS = CONSTANT+LNSMOLT_5+LHBTFFEB+HARP2

Diagnostics:

Dep Var: ISW_RECRUITS N: 17 Multiple R: 0.94334 Squared multiple R: 0.88989

Adjusted squared multiple R: 0.86448 Standard error of estimate: 7.07600

Effect	Coefficient	Std Error	Std Coef	Tolerance	t	P(2 Tail)
CONSTANT	123.26400	61.68057	0.0	.		1.99843 0.06703
LNSMOLT_5	-8.97095	3.55762	-0.24202	0.91945	-2.52162	0.02553
LHBTFFEB	6.47529	1.05701	0.68324	0.68092		6.12604 0.00004
HARP2	-0.56372	0.25091	-0.24987	0.68479		-2.24671 0.04267

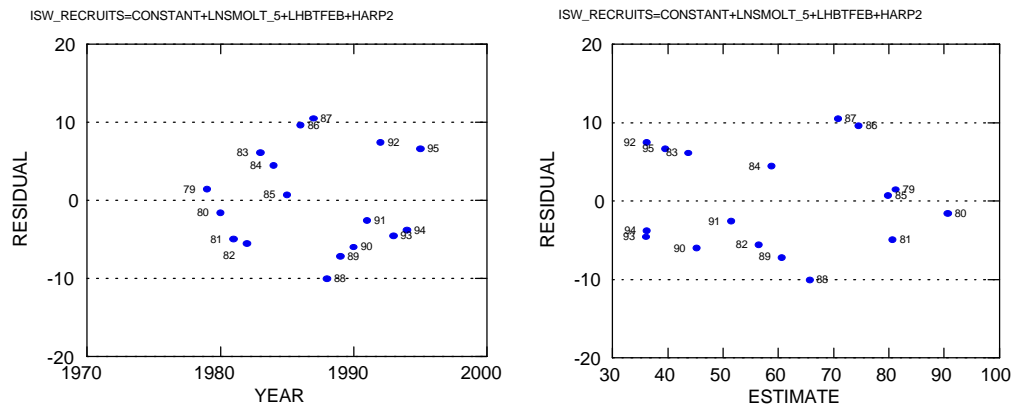
Analysis of Variance

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
Regression	5260.60282	3	1753.53427	35.02176	0.00000
Residual	650.90799	13	50.06985		

Durbin-Watson D Statistic 1.617

First Order Autocorrelation 0.157

The residuals of this model showed no temporal or scalar trends.



Discussion

Evidence of predation of Atlantic salmon by seals is both absolute and circumstantial. Direct but sparse evidence of predation of salmon was observed in the Northern Gulf of St. Lawrence (Hammill and Stenson 1997). There is no similar evidence of predation by seals on salmon in the 2J3KL, Newfoundland coast or Flemish Cap areas. The coincidence of salmon and seals in these areas is well established and there is no reason to think that if predation occurs in the Gulf of St. Lawrence then predation would not occur in the offshore areas. This hypothesis does not require that seals are dependent on salmon for any portion of their diet. The hypothesis requires only that there may be a preference for salmon when encountered and once conditioned to prey on salmon predation continues until encounters are rare enough that there is no benefit to the predator.

This analysis used only Harp seals as the seal population variable. This was because harp seals represent 82% of the total consumption of prey in the Northwest Atlantic. The population increase of Harp seals has been about 4.8% year⁻¹. Populations of the other species have also increased in the time period (Hammill and Stenson 1997) and would be expected to have the same significance in the models without direct evidence of predation. Hooded seals, a species coincident with non-maturing sea ages of salmon and with harp seals for half of a year, primarily prey on bottom dwelling fish (*ibid*). However, as Hammill and Stenson (1997) state the diet of hooded seals in the offshore area is assumed from that observed in the nearshore area. Gray seals and harbour seals are not as prevalent in the northern areas and therefore do not represent the same potential as harp seals to account for the coherence in recruitment of North American salmon. The more southern distribution of gray seals and therefore exposure to less of the total North American stock of salmon decreases their potential predation on NA salmon. In fact, their predation on a portion of the returning salmon could result in a dissolution of the coherence in the recruitment of NA salmon. The possibility also exists that harp seals are only a surrogate for some other predator or environmental feature that reduces recruitment and increases the size distribution of one-sea-winter recruits.

One of the principal requirements for this hypothesis to be true is predator preference and predator attraction. Underlying this predator preference must be an energetic or physiological reason. One hypothesis for a physiological reason influencing predator preference is osmoregulation of marine mammals. Marine mammals do not drink fresh water and must maintain homostasis (principally salt balance in the blood and lymphatic systems) in a marine aquatic environment, principally through diet. Direct consumption of prey high in moisture content and low in salt as well as the consumption of prey high in fats readily oxidized to produce water (Ridgway 1972) may be a reason for a preference for Atlantic salmon.

A corollary of the hypothesis presented here is that predation results in selective removal of the smaller sizes of salmon. This effect is first observed in reduced size-at-age of one-sea-winter returns. Also, if this selection affects salmon destined to all ages-at-maturity then increased size of one-sea-winter returns is a precursor of decreased numbers of two-sea-winter returns. A form of this model has been used to forecast the two-sea-winter returns to Mactaquac on the Saint John River (Marshall MS 1992). In this model two-sea-winter salmon are forecast from the numbers of one-sea-winter returns and the length of one-sea-winter salmon. The coefficient for length is negative. Interpretation for this effect has been suggested as change at age-of-maturity caused by annual change in growth rate. The predation effect is an equally plausible explanation that is compatible with the high heritability of age-at-maturity observed among stocks of Atlantic salmon.

The exclusion of the 1977 smolt class from these models could be based on the significance of residuals alone. Parameters for the models presented here could be estimated through iterative re-weighted least squares with these values included. However, the recruits from the 1977 year class were smaller and of lower condition when measured at Morgan Falls, LaHave River (Amiro *et al.* MS1998). This suggests other mechanisms for reduced marine survival may have acted on the 1977 smolt class. Inclusion of future or of past observations of reduced size-at-return may provide data to examine hypotheses to explain these observations.

Forecasts of returns for 1997 to 1999 were not made for the models presented. Forecasts were provided by Amiro (MS1998) using YEAR as a variable to account for the monotonic decline in marine survival. Because these forecasts utilize the winter habitat area they remain plausible as long as there is a monotonic increase in the population of seals. There is no evidence that the population of seals did not continue to increase in 1997 and in 1998. The models presented here attain about the same precision as those containing the YEAR variable. Models using seal population and habitat have the advantage of forecasting turning points in marine survival of salmon resultant of decreased predation. These turning points can both be the result of decreased seal populations, increased habitat area or the interaction of these variables. The 1998 winter may be one of these points. Over-flights of the North Atlantic (J. Conway pers.

comm.)³ during the first week of April 1998, reported the ice front to be as far north as area 2G (mid Labrador coast). According to the hypothesis and models presented here interaction of post-smolt salmon, with at least a portion of the harp seal population, will be less in 1998 than in previous years and increased recruitment is forecast.

The salmon recruitment models presented here and by Amiro (MS1998) both resolve some on-going problems and propose some new concepts. The present ICES pre-fishery abundance model cannot include (and remain significant) the Gulf of St. Lawrence stock. This would imply that Gulf of St. Lawrence salmon recruitment is out of synchrony with the rest of the NA. Yet, the Gulf of St. Lawrence is on average 23% of the NA 1SW recruitment and 48% (1992 to 1995) of the MSW recruitment. The models proposed here use all NA recruits and resolve this dilemma.

The pre-fishery abundance model of ICES is a proportional recruitment model for non-maturing salmon only. The ICES model assumes that more spawners and larger habitat will result in more MSW recruits. The higher spawning escapements, associated with the closed commercial fisheries, were therefore expected to result in higher recruitment. Returns since 1989, and particularly 1997, did not follow that forecast. The biological interpretation of proportional recruitment is difficult to accept and without fishing mortality, recruitment is expected to rise proportionately. Apparently this has not occurred since the closure of the commercial Atlantic salmon fisheries prosecuting North American Atlantic salmon. The models proposed here account for this lack of recruitment.

The models presented here and those of Amiro (MS 1998) propose depensatory recruitment in the marine environment and compensatory effect in the freshwater environment. While compensation, a limit, may occur in the freshwater phase of the life cycle, it is difficult to accept that for a relatively rare species like Atlantic salmon, that marine survival is compensatory but rather is dependent on other factors, like predators, and is therefore depensatory. The combination of these successive recruitment stages results in a non-linear response. In the linearized integrated form of the recruitment model, the negative parameter i.e. - LNSMOLT_5 captures the predator attraction effect. At low prey abundance there is little, but always some, predator effect. At high prey abundance there is an increasing predator affect. The ecological mechanism for this response is discussed in Hilborn and Walters (1992). Multi-stage recruitment models have been proposed by Beverton and Holt (1957), Paulik (1973) others (Peterman 1977, 1980) but have not been previously applied to recruitment of NA salmon.

As in most stock and recruitment models it is difficult to verify the mechanism let alone the parameter specifications. In a ideal situation one would independently control the spawning stock, predator field and the environment. Thus recruitment would be validated for all conditions of the variables in the model. Since a controlled experiment is all but impossible we can only observe the state of the variables in the model, make forecasts and keep track of the recruits. The most disconcerting feature of the condition of the variables is the linear nature of the seal population data. Variance in the population of seals would greatly assist in testing the ability of the model to predict recruitment. More observation and therefore verification of predation by seals on free swimming salmon would lend considerable credence to this hypothesis, however, lack of positive observations of predation will not negate the models proposed.

Acknowledgments

Mike Hammill provided the recent population estimates of harp seals and critical review of the manuscript. Dave Reddin provided the recent estimates of the marine habitat area for Atlantic salmon. Larry Marshall provided critical review of the manuscript and suggested including

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discussion on how these models differed from those currently used by the ICES, Working Group on North Atlantic Salmon. David Cairns suggested modifications to assist in clarifying the points being made. Jim Eddington reviewed an earlier draft and suggested exploring physiological reasons for predation. Karen Rutherford edited the manuscript. I thank all those who contributed.

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Table 1. Population of harp seals, natural logarithm of the annual Atlantic salmon smolt migration (Amiro 1998), area of marine winter habitat for salmon 1973 to 1997 and one and two-sea-winter recruitment of North American salmon.

Year	Harp seal population	LnSmolt_5 year i-1	Winter habitat area		1SW	MSW
			February	March	recruits	recruits
			yr i area/100	yr i area/100	10,000's yr i + 1	10,000's yr i + 2
1973	1,868,240	15.53	17.08	18.96	68.7441	69.4437
1974	1,938,910	15.74	18.62	17.46	67.3352	64.9807
1975	1,979,910	.	18.27	18.42	80.9530	72.7627
1976	2,013,990	15.62	16.76	19.53	78.3601	64.5753
1977	2,071,560	16.51	19.15	19.94	61.5674	51.2912
1978	2,157,270	16.46	19.51	19.79	38.7051	29.0946
1979	2,240,140	15.73	20.58	19.99	58.7919	65.6087
1980	2,317,780	16.38	18.23	20.88	82.7319	55.8849
1981	2,388,230	15.93	19.12	18.07	89.1153	52.6070
1982	2,454,390	15.49	17.03	16.21	75.6969	44.1659
1983	2,559,330	16.06	14.16	13.69	50.8609	23.5090
1984	2,762,640	16.20	12.57	12.09	49.8742	25.0709
1985	2,988,950	15.48	14.1	13.97	63.2386	41.4498
1986	3,230,820	14.98	16.88	15.47	80.5963	45.1932
1987	3,495,440	14.98	16.27	14.71	84.1416	39.2142
1988	3,711,760	15.77	16.98	16.22	81.2815	31.6084
1989	3,865,670	15.84	16.42	15.52	55.6459	24.0807
1990	3,920,020	15.37	15.03	14.91	53.3976	21.7980
1991	4,032,020	15.96	13.57	15.19	39.2023	26.1713
1992	4,178,060	15.34	13.81	13.78	48.8662	15.7727
1993	4,326,470	16.02	12.52	12.42	43.6385	11.7143
1994	4,525,150	16.47	13.29	13.73	31.4702	13.1175
1995	4,697,290	16.20	13.1	12.79	32.4109	12.8388
1996	4,878,520	16.87	14.7	14.19	46.2052	.
1997	4,904,330	16.97	15.94	.	.	.
1998		16.44			.	.

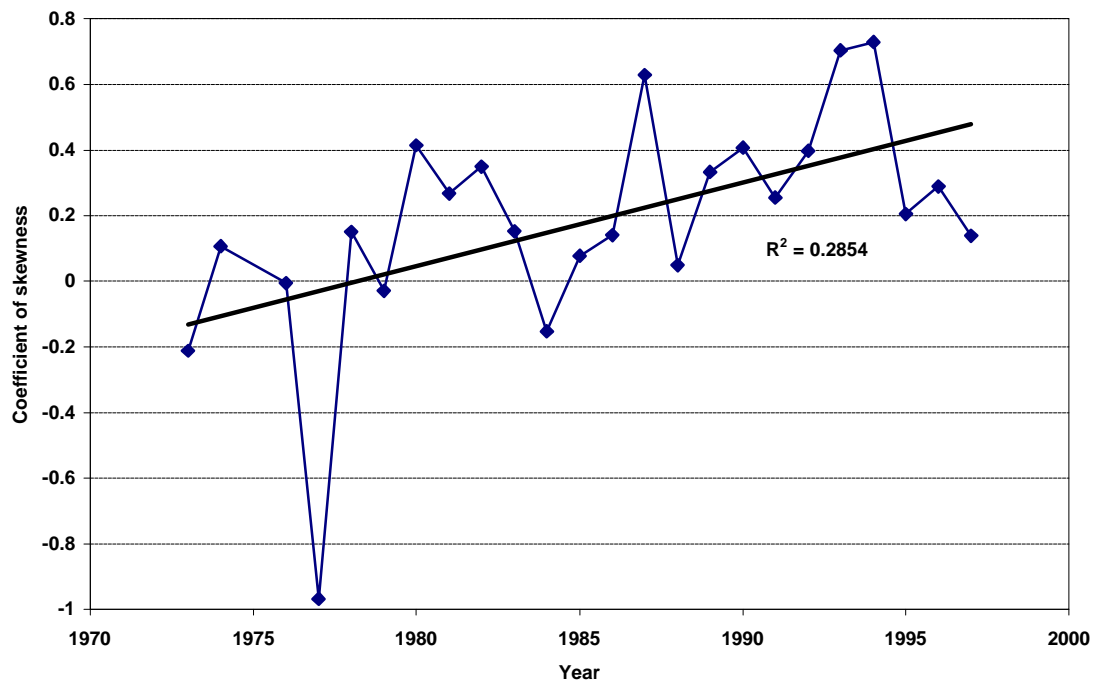


Figure 1. Coefficient of skewness of the fork length of age 2.1 (freshwater.seawinters) Atlantic salmon returning to Morgan Falls, LaHave River, Nova Scotia, for the years 1973 to 1997. The trendline is significant at $p=0.007$.

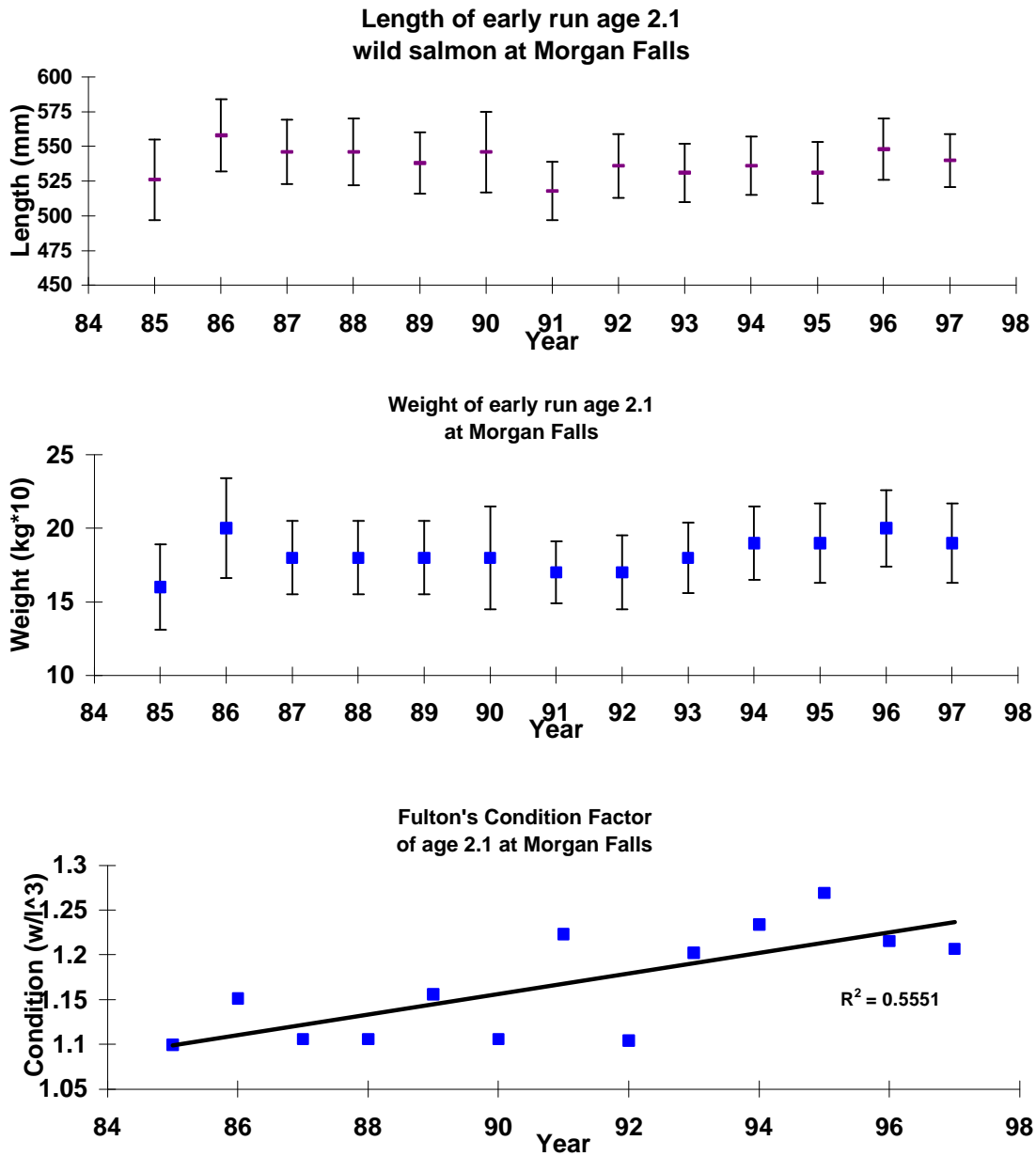


Figure 2. Length, standard deviation of length, weight, standard deviation of weight and Fulton's condition factor of early run age 2.1 (freshwater-sea winters) wild Atlantic salmon measured at Morgan Falls fishway, 1984 to 1997.