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### Model estimates of harp seal population trajectories in the Northwest Atlantic

by

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#### ABSTRACT

Harp seal catch-at-age data from the Northwest Atlantic, together with age specific pregnancy rate data, allow an age structured population model to be fit to field estimates of pup production. Field estimates of pup production comprise five mark-recapture estimates and two aerial survey estimates. Model fits to alternative subsets of these data give a range of estimates of pup production in the initial year of the model and natural mortality rate. Models fit to field estimates that include the 1990 aerial survey provide estimates of the 1990 pup production which are in close agreement to each other. All model fits provide similar estimates of the ratio of total population to number of pups for 1990. There is an indication of population growth in recent years in all model fits, although there is some variability, both among models fitted to different subsets of the data and within individual trajectories.

# RÉSUMÉ

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Les données sur les captures de phoque du Groenland en fonction de l'âge dans le Nord-Ouest de l'Atlantique, combinées aux données sur les taux de gravidité spécifiques de l'âge, permettent d'ajuster un modèle de population fondé sur l'âge aux valeurs estimées sur le terrain de la production de jeunes phoques. Les estimations sur le terrain de la production de jeunes phoques comprennent cinq estimations provenant d'expériences de marquagerecapture et deux estimations obtenues à partir de relevés aériens. Les ajustements du modèle à des sous-ensembles différents de ces données donnent une étendue de valeurs estimées pour la production de jeunes phoques pour l'année initiale du modèle et le taux de mortalité naturelle. Les ajustements du modèle aux estimations sur le terrain comprenant le relevé aérien de 1990 fournissent des valeurs estimées de la production de jeunes phoques en 1990 qui concordent étroitement entre elles. Tous les ajustements du modèle donnent des valeurs estimées semblables du rapport de la population totale au nombre de jeunes phoques en 1990. On trouve des indications qu'il y a eu croissance de la population aux cours des dernières années dans tous les ajustements du modèle, bien qu'il y ait une certaine variabilité tant entre les modèles ajustés aux différents sous-ensembles de données qu'à l'intérieur des trajectoires individuelles.

### 1. INTRODUCTION

The harp seal population in the Northwest Atlantic has been harvested for centuries. Commercial harvest, mainly of pups and some adults on the whelping ice patches in the Gulf of St. Lawrence (Gulf) and off the coast of north east Newfoundland (Front), increased in the early 19th century (Templeman 1966) and catches have remained high during most of the present century (Anon 1986). Regulations imposed since 1971 and a collapse in the market in 1983 has resulted in a cessation of the white coat hunt and a substantially reduced harvest in recent years, but commercial sealing is thought to have seriously reduced the population prior to this (Anon 1986). Since 1982 a status quo TAC of 186,000 animals has been imposed, although over the last 5 years the total annual recorded harvest has averaged only about 80,000 animals (including estimates for Canadian Arctic and Greenland catches).

Following reduced harvests in recent years, it is a reasonable expectation that the harp seal population in the Northwest Atlantic is recovering from low population sizes in the 1960s and 1970s. Mark-recapture and aerial survey studies provide point estimates of pup production for specific years but many different population trajectories can be drawn through these data. The number of alternative plausible trajectories can be constrained by taking into account catch-at-age data and age specific pregnancy data in a dynamic, age-structured model of the harp seal population. The most likely trajectory and the confidence in this trajectory can be estimated by fitting to the mark-recapture and aerial survey estimates of pup production. Such estimates and associated estimates of replacement yield are likely to be useful in developing management policy for the harp seal population in the Northwest Atlantic.

In this paper published mark-recapture and aerial survey estimates of pup production are briefly reviewed, updated catch-at-age and age specific pregnancy values are presented, and a modified version of the Roff-Bowen population model (Roff and Bowen 1983) is described and fit to various combinations of field estimates of pup production. Results are compared and discussed. Cadigan and Shelton (in prep.) provide estimates of confidence intervals on trajectories and replacement yields.

### 2. SURVEY ESTIMATES

Mark-recapture estimates of pup production are available for 1977-80 and for 1983 (Bowen and Sergeant 1983, Roff and Bowen 1986, Warren 1991). The 1977 and 1983 estimates must be treated with particular caution because the former is based on pups marked only in the Gulf while the latter is from short-term recoveries that would not have allowed adequate mixing. An aerial survey is available for the

Front in 1983 (Myers and Bowen 1989). This estimate was increased by 20% to account for bias (Myers and Bowen 1989) and by a further 37% to account for the ratio of pups in the Gulf and Front estimated from short term tag recoveries in that year (Bowen and Sergeant 1983). A further aerial survey estimate of pup production for Front and Gulf herds is available for 1990 (Stenson et al. 1991). Estimates of pup production and associated standard error are presented in Table 1.

In a critical review of the mark-recapture estimates, Warren (1991) observed that several of the assumptions on which this estimator is based are violated in it's application to the Northwest Atlantic harp seal pup production, and that the estimates should be used with caution. Similarly, with respect to the aerial survey estimates, Stenson et al. (1991) suggest that there are several problems associated with the application of aerial survey techniques to harp seal pup production. In 1990 the aerial survey was designed so as to reduce the possible sources of bias by using a combination of visual and photographic techniques, extensive reconnaissance, coverage of areas outside of the whelping concentrations, and by determining the temporal distribution of births (Stenson et al. 1991).

# 3. CATCH AT AGE

Catch at age data going back as far as 1952 exists for 5 types of seal hunts (Bowen 1982; E.A. Perry, G.B. Stenson and W.J. Penny, Department of Fisheries and Oceans, St John's, unpublished manuscript). They are the (i) large vessel hunt, (ii) longliner hunt, (iii) inshore net catch and shooting, (iv) Greenland hunt and (v) Canadian Arctic hunt. The inshore net catch and shooting harvest is combined in this analysis as "net" catch. Because the model described below treats a year as 1 April to 31 March, the net catch, which is taken at the beginning of the calendar year, is assigned to the previous model year. The total catch-at-age in model year t is therefore the sum of the catches from large vessels, longliners, Greenland and the Canadian Arctic in calendar year t and net catches in calendar year t+1 (Table 2, 1965-90).

Several problems with respect to missing data exist in constructing a time series of catch by age for the Northwest Atlantic harp seal population (E.A. Perry, G.B. Stenson and W.J. Penny, Department of Fisheries and Oceans, St John's, unpublished manuscript). Catch data for Greenland and the Canadian Arctic are missing for recent years. For the Canadian Arctic the 1982 value of 4,881 given in Roff and Bowen (1986) has been used in all subsequent years. For Greenland an annual value of 18,000 has been used from 1988 onwards. The catch of 11+ year old seals in the Greenland hunt up to the mid 1970s and 10 year olds thereafter have been lumped into single "plus" age classes. Few age frequencies exist for breaking down Greenland and Canadian Arctic catches.

In order to examine the characteristics of the data, catch in thousands of individuals are plotted in various ways by age and year for each type of hunt as well as the total hunt (Figs. 1-5). It can be noted that the bulk of the harvest prior to 1984 was made by large vessels and, to a lesser extent, longliners, taking predominantly pups (Figs. 1 and 2). The net catch data does not include any pups and is combined with the longliner catch after the mid-1980s. The large vessel catch is discontinued in the late 1980s. It can be seen from the log-transformed data (Fig. 4) that there is a decline in the numbers of 1+ seals caught by the large vessel hunt up to its cessation. In general, variability in catches appears to increase with age and cohort effects are not clearly visible in the data.

A more detailed view of the large vessel, net and longliner catches are given in Figs. 5a-c. There is a possible cohort effect in the net catch in that some strong year classes apparent as 1 year-old seals in the mid 1970s can be seen moving through the older age classes into the early 1980s. However, much of the remaining variability appears to be associated with year effects or interaction effects between year and age. In order to interpret this variability, the reliability of the estimated age composition needs to be examined and conditions related to the harvest need to be accounted for (e.g. method, duration, ice conditions, TA C restriction etc.). In particular, data manipulation through the use of single age compositions and/or constant harvests for extended periods needs to be critically examined. It is possible that more rigorous statistical methods could be employed to reconstruct missing data.

# 4. PREGNANCY RATES

Reproductive samples were collected in late term to reduce the bias caused by inter-uterine mortality. Proportion pregnant at age a in year t therefore indicates the rate of pup production by females in year t. Roff and Bowen (1983) presented data for the period 1965-70, 1978 and 1979 for ages 3 to 7+. Unpublished data are also available from Science Branch, Newfoundland Region, Department of Fisheries and Oceans for the period 1979 to 1990. These data have been combined in Table 3. Sample sizes, where available, are given in Table 4.

There is a pattern within age over years in the pregnancy rates (Table 3). In the 1960s no females aged 3 were pregnant. The proportion of 4 and 5 year old females pregnant in the 1980s appeared to be higher than in the 1960s. There is the possibility of slightly lower pregnancy rates among 6 and 7+ females in recent years.

It would be useful if the missing data in the annual age specific pregnancy table could be estimated by some method. Cook et al. (1985) used an assumed time series of age at maturity and age-aggregated pregnancy rates as input to their model. Their time series had an increasing trend in pregnancy rate between 1952 and 1967 and thereafter constant values, and a constant age at maturity between 1952 and 1970, and thereafter decreasing values. Roff and Bowen (1983) used a linear fit to transformed percentage pregnant for ages 5 and 6 and constant values for ages 3, 4 and 7+ to estimate pregnancy rates for their model. This approach is no longer applicable because the pregnancy rate in the older age classes shows some levelling off or even a decline in the more recent years.

The following approaches for providing estimates for the missing pregnancy rate logits were explored: (i) multilinear regression against dummy variables for age and year; (ii) analysis of covariance with age as a continuous variable and cohort as a class variable; (iii) analysis of variance with age and cohort effects; (iv) autoregression models. (i) gave increasing trends against year, and therefore could not account for the relative constancy or possible declines in recent years; (ii) was significant and provided estimates of 35 of the missing 50 data, however estimates for the missing period in the 1970s were considered unacceptably low and the residuals were patterned; (iii) gave residuals which appeared to be nearly random, but again estimates of missing values for the 1970s were considered to be unacceptably low for the older age classes; (iv) resulted in a significant autoregressive model for 5 yr-olds only.

After concluding that the above methods were inappropriate for filling in the missing data, linear interpolation of logits over years within age groups was carried out using all data with sample size of 5 or greater. Data with sample sizes of less than 5 were considered missing data. The resulting table of values (Table 5) was used in subsequent model fitting.

### 5. MODEL ESTIMATES OF TRAJECTORIES

A method based on the model of Roff and Bowen (1983) was developed to estimate a time series of numbers at age. The model estimates are obtained from catch-at-age and age specific pregnancy rate data, together with a natural mortality parameter an a nuisance parameter used to construct initial numbers-at-age. The basic model is

$$N_{a,t} = (N_{a-1,t-1}e^{-\frac{m}{2}} - C_{a-1,t-1})e^{-\frac{m}{2}} \text{ for } A > a > 0$$

$$N_{0,t} = \sum_{a} N_{a,t}f_{a,t}$$
(1)

where  $N_{a,t}$  is the number at age a in year t, A is a "plus" age class (i.e. all animals aged A and older lumped), m is the annual instantaneous natural mortality rate,  $f_{a,t}$  is the per capita pup production rate of age a animals in year t assuming 50% of adults at each age are female. The year is considered to commence on 1 April at which time pups are born and the field estimate of the number of pups is carried out. For the plus age class A

$$N_{A,t} = (N_{A,t-1}e^{-\frac{m}{2}} - C_{A,t-1})e^{-\frac{m}{2}} + (N_{A-1,t-1}e^{-\frac{m}{2}} - C_{A-1,t-1})e^{-\frac{m}{2}}$$

In order to obtain the initial population vector, let  $\phi$  be a parameter representing the number of newborn pups in  $t_0$  (in this case 1965). If the proportions at age of the 1+ population in year  $t_0$  is known, then  $N_{1+}$  can be estimated from

$$\phi = \sum_{a} p_{a,t_0} f_{a,t_0} N_{1+}$$

and solving for  $N_{1+}$ 

$$N_{1+} = \frac{\phi}{\sum_{a} p_{a,t_0} f_{a,t_0}}$$
(2)

The initial population vector can now be computed from  $N_{1+}$  and  $p_{a,t}$ . Using this method,  $p_{a,t}$  for 1965 was set to the 1967 proportions at age calculated by Roff and Bowen (1983). Although this is an arbitrary approach, the model estimates are not sensitive to the initial population vector beyond about the first 10 years. Nevertheless, a more defendable approach for obtaining the initial population vector is being developed (Cadigan and Shelton, in prep.) based on the approach of Cook et al. (1985).

The model given in (1) was transformed into a standard nonlinear regression form by making each  $N_{a,t}$  a function of  $\phi_t f_{a,t}$  and  $C_{a,t}$  by recursively substituting  $N_{a-1,t-1}$  in (1). The parameters were then estimated by weighted least squares using PROC NLIN in SAS (1990), fitting to the field estimates of  $N_{0,t}$  and using the estimated variances of the survey estimates as weights. The parameter estimates are maximum likelihood estimates under the assumption that field estimates of  $N_{0,t}$  are normally distributed.

The model contains no density compensation effects, so that with constant catch and pup production rate, the model population can only decrease exponentially, stay constant, or increase exponentially when projected forward in time. However, field estimates of annual pup production rate at age are used in the estimation, so that a data-driven compensatory response is feasible (e.g. if pup production rates decline at high population size).

In fitting to mark-recapture and aerial survey estimates of pup production, it is not possible to account for biases in the different estimates because the magnitude and, in some cases, the direction of these biases are unknown. In an attempt to examine the robustness of estimates of trajectories, several alternative combinations of field estimates were used (Models a-f, Table 6).

The results from these fits are summarised in Table 7 and model trajectories of pup production are plotted in Fig. 6 together with the field estimates of pup production. Estimates of pup production in 1965 range from 360,000 to 650,000. The highest estimate comes from model (e) which fits to mark-recapture estimates (excluding 1977) together with the 1990 aerial survey. Because of the correlation between initial pup production and natural mortality rate, this model also has the highest mortality rate (m=0.136). Model estimates of pup production in 1990 range from 580,000 to 1,200,000 pups compared with an aerial survey estimate of 580,000 pups. Essentially models which include the 1990 estimate fit this data point well, whereas models which do not include the 1990 estimate in the fit, predict a 1990 pup production in excess of the survey estimate. In other words, the most recent survey indicates that the population is not growing as fast as would have been predicted on the basis of the data up to, but not including, 1990. The highest estimate of pup production comes from model (b) which fits to only the first 4 mark-recapture estimates. This model also gives the highest estimate of total population size, over 6 million, compared to the lowest estimate of little more than 3 million. Those fits using the 1990 aerial survey value give estimates in close agreement with each other, about 3 million animals. Of some interest is the small range in model estimates of the ratio of the total population to the pup production, 5.4 to 5.5.

# 6. DISCUSSION

The catch-at-age data, together with age specific pregnancy rate data, allow an age structured population model to be fit to field estimates of harp seal pup production. There is a relatively wide range in model estimates of pup production in the initial year and natural mortality rates from model fits to different subsets of the field estimates of pup production. Models fit to field estimates which include the 1990 aerial survey value provide estimates of the 1990 pup production which are in close agreement. All model fits provide similar estimates of the ratio of total population to number of pups for 1990. There is an indication of population growth in recent years in all model fits, although there is some variability, both among models fitted to different subsets of the field estimates of

pup production, and in year to year changes in population size within each trajectory. Models (e) and (f) show the least evidence of population growth. In all the trajectories, the model estimate of the 1989 pup production is low, a consequence of a large 1988 harvest and low 1989 pregnancy rates.

The small sample size for estimating pregnancy rates is problematic. The pregnancy rate data is pivotal in the estimation and attempts should be made to increase the sample size in future years.

Future modeling effort will be devoted to a more rigorous procedure for obtaining the age composition in the initial year, and to the estimation of confidence intervals on the trajectories (Cadigan and Shelton, in prep.). Attention will also be devoted to determining the probability that the population has been increasing in recent years, and to estimating the current replacement yield of the population.

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Table 1. Mark-recapture and aerial survey estimates of pup production and
associated error (see text for origin of estimates). Under Type, MR refers to mark
recapture and AS refers to aerial survey.

Year	Estimate	Standard error	Туре	
1977	318.000	48,000	MR	
1978	497,000	34,000	$\mathbf{MR}$	
1979	478,000	35,000	MR	
1980	475,000	47,000	MR	
1983	534.000	33,000	$\mathbf{MR}$	
1983	386,000	81,000	AS	
1990	577,900	38,800	AS	
	Year 1977 1978 1979 1980 1983 1983 1983 1990	YearEstimate1977318,0001978497,0001979478,0001980475,0001983534,0001983386,0001990577,900	YearEstimateStandard error1977318,00048,0001978497,00034,0001979478,00035,0001980475,00047,0001983534,00033,0001983386,00081,0001990577,90038,800	YearEstimateStandard errorType1977318,00048,000MR1978497,00034,000MR1979478,00035,000MR1980475,00047,000MR1983534,00033,000MR1983386,00081,000AS1990577,90038,800AS

Table 2. Total annual catch-at-age for harp seals in the Northwest Atlantic for the period 1965-90 (see text for details).

Ages								
Year	0	1	2	ັ3	4	5	6	7+
1965	188184	12952	6501	5317	5139	6248	5921	15042
1966	255874	14385	11278	5189	4849	5206	5133	30654
1967	280257	14683	6826	2992	2452	2931	3784	24932
1968	160595	7530	4865	3590	2371	2225	1766	21879
1969	237103	21346	3905	3422	2722	3099	2200	24844
1970	221075	9399	7603	2865	2345	2204	1352	13307
1971	212854	8281	3098	2068	1328	1011	745	6430
1972	120263	4862	2798	1745	1475	746	657	5314
1973	103435	7060	4875	3264	2575	3583	1845	9468
1974	119413	13192	7783	3370	2556	2407	2771	9506
1975	144449	14183	6247	3276	1886	1371	1282	6906
1976	136974	15565	7691	4166	2563	743	395	2838
1977	134893	9222	6831	6580	5066	3075	1702	5545
1978	121058	18409	11010	5958	3938	2532	1846	<b>4849</b>
1979	139200	16161	7580	4345	2691	2009	1459	6195
1980	136182	18205	9770	6269	4249	3305	2243	9178
1981	184593	9164	5038	3830	2409	1887	1748	7018
1982	153096	14996	7195	3444	1727	1307	715	4564
1983	58544	7608	4576	2714	1416	1150	943	4808
1984	31850	5906	5315	2806	1729	921	722	3966
1985	21690	6725	4913	2517	1222	747	591	3956
1986	28240	4747	3366	2412	1210	662	562	3548
1987	40951	5686	4139	3369	2234	1171	1012	6407
<b>19</b> 88	75108	11191	9867	5613	3553	1970	1716	7909
1989	62037	7228	5394	3501	2220	1547	1095	4933
1990	41346	9374	6217	5265	4181	3548	1876	9296

Table 3. Proportion of late term pregnant females at ages 3 to 7+. Note, this table includes sample sizes as small as only one female (see Table 4 for sample sizes).

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Yr	3	4	5	6	7+
65	0.000	0.033	0.114	0.541	0.837
66	0.000	0.000	0.111	0.353	0.850
67	0.000	0.000	0.211	0.606	0.901
68	0.000	0.000	0.316	0.700	0.881
69	0.000	0.004	0.160	0.438	0.880
70	0.000	0.000	0.231	0.500	0.863
71	•	•	•		•
72	•	•	•	•	•
73	•	•		•	•
74	•	•	•	•	•
75	•	•	•	•	•
76	•	•	•	•	•
77	•	•	•	•	•
78	•	•	•	•	•
79	0.000	•	0.000	1.000	0.000
80	•	0.500	1.000	•	0.833
81	0.250	0.400	0.667	0.889	0.737
82	0.000	0.200	0.800	1.000	0.923
83	•	•	•	•	•
84	0.000	0.333	0.400	1.000	1.000
85	•	•	1.000	0.000	1.000
86	0.100	0.091	0.667	1.000	0.818
87	0.167	0.375	0.750	1.000	0.787
88	0.000	0.000	0.429	0.750	0.955
89	0.000	0.000	0.250	0.000	0.714
90	0.077	0.250	0.636	0.667	0.878

Table 4.	Sample size for	or determining	late term	pregnancy	for ages 3	3 to 7+.	Data
prior to 1	1979 are not av	vailable.					

Yr	3	4	5	6	7+
				·	
65	•	•	•	•	•
66	•	•	•	•	•
67	•	•	٠	•	•
68	•	•	•	•	•
69	•	•	•	•	•
70	•	•	•	•	•
71	•		•		•
72	•		•		•
73	•	•	•	•	•
74		•		•	•
75	•				•
76			•		
77					
78					
79	1	Ó	1	1	2
80	Ō	2	1	Ō	12
81	4	5	3	9	19
82	3	5	5	1	13
83	Õ	Ō	Ō	ō	0
84	4	3	5	š	1
85	Ō	ŏ	1	1	1
86	10	11	ģ	1	11
87	94	8	4	5	61
88	7	Ř	7	4	22
20 20	11	g	4	1	7
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50	τŋ	14	TT	J	41

Table 5. Pregnancy values used in the model fits. Samples of less than 5 females were set to missing. The table includes interpolated values for missing values (see text).

Year	3	4	Ages 5	6	7+
65	0.00000	0.03300	0.11400	0.54100	0.83700
66	0.00000	0.00000	0.11100	0.35300	0.85000
67	0.00000	0.00000	0.21100	0.60600	0.90100
<b>6</b> 8	0.00000	0.00000	0.31600	0.70000	0.88100
69	0.00000	0.00400	0.16000	0.43800	0.88000
70	0.00000	0.00000	0.23100	0.50564	0.86300
71	0.00000	0.00000	0.26913	0.57307	0.85814
72	0.00000	0.00000	0.31100	0.63789	0.85314
73	0.00000	0.00000	0.35622	0.69806	0.84799
74	0.00000	0.00160	0.40415	0.75211	0.84269
75	0.00000	0.00319	0.45399	0.79927	0.83725
76	0.00000	0.00637	0.50476	0.83937	0.83165
77	0.00000	0.01266	0.55544	0.87274	0.82590
78	0.00000	0.02500	0.60500	0.90000	0.82000
79	0.00000	0.07060	0.66068	0.89641	0.82677
80	0.00000	0.18370	0.71225	0.89271	0.83333
81	0.00139	0.40000	0.75884	0.88889	0.73684
82	0.00332	0.20000	0.80000	1.00000	0.92307
83	0.00795	0.16584	0.62020	1.00000	0.90375
84	0.01888	0.13652	0.40000	1.00000	0.88021
85	0.04420	0.11169	0.53590	1.00000	0.85186
86	0.10000	0.09090	0.66667	1.00000	0.81818
87	0.16667	0.37500	0.55051	1.00000	0.78688
88	0.00000	0.00000	0.42857	1.00000	0.95454
89	0.00000	0.00000	0.53394	1.00000	0.71429
90	0.07692	0.25000	0.63636	0.66667	0.87805

Table 6.	Combinations	of field	estimates	of pup	production	from	Table	1 used	l in
the fits o	f models a-f in	Table 7	and Fig. 6		-				

Model	Field estimates used
a b c d e	6, 7 1, 2, 3, 4 2, 3, 4, 5 1, 2, 3, 4, 5 2, 3, 4, 5, 7
f 	1, 2, 3, 4, 5, 7

Table 7. Summary of the model estimates from different subsets of the markrecapture and aerial survey field estimates of pup production. See Table 6 for an explanation of the alternative models a-f.

Model	N <sub>0</sub> (1965)	m	$N_0(1990)$	Tot N (1990)	Tot $N/N_0$ (1990)
 a	363,570	0.084	577,900	3115,596	5.391
b	371,272	0.072	1160,238	6428,254	5.540
С	511,532	0.111	744,275	4072,938	5.472
d	480,288	0.105	767,701	4204,361	5.477
е	653,364	0.136	582,002	3156.361	5.423
f	592,543	0.128	595,507	3230,900	5.425



Fig. 1. Catch-at-age data from different sectors of the harvest for harp seals in the Northwest Atlantic, 1952-90, plotted on the same scale.



Fig. 2. Catch-at-age data from different sectors of the harvest for harp seals in the Northwest Atlantic, 1952-90, plotted on individual scales.



Fig. 3. Catch-at-age data from different sectors of the harvest for harp seals in the Northwest Atlantic, 1952-90, scaled by year totals.



Fig. 4. Logarithm of catch-at-age from different sectors of the harvest for harp seals in the Northwest Atlantic, 1952-90.



Fig. 5. Catch by age class for harp seals in the Northwest Atlantic over the period 1952-90 for (a) the large vessel catch, (b) net catch, and (c) the longliner catch.



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Year

Fig. 6. Model estimates of harp seal pup production trajectories for the period 1965-90 from fits of an age structured population model to different subsets of the field estimates of pup production (see text for details). Note that panel b has a different scale on the ordinate than the other panels.

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