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Reproductive rates of Northwest Atlantic harp seals, 1954-2007

# Taux de reproduction des phoques du Groenland de l'Atlantique Nord-Ouest, de 1954 à 2007

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#### ABSTRACT

Obtaining accurate estimates of fecundity are critical for estimating the population dynamics of a species. Data on pregnancy rates of Northwest Atlantic harp seals have been collected since the 1950s. However, sample sizes were highly variable with little or no reproductive data for many year-age combinations. To obtain the data required to estimate total abundance, we used a non-parametric regression estimator to estimate the expected annual age-specific pregnancy rates using data collected up to 2007. Pregnancy rates among 4 year olds remained low (<10 %) throughout the time period. Seals aged 5 and 6 showed a similar pattern; age-specific pregnancy rates initially increasing during the 1970s, but declined by the mid 1980s to levels similar to, or lower than, those seen in the 1960s. Seals 7 years of age and older remained high until the mid 1980s when they declined to their current low levels. Estimates of recent reproductive rates are slightly lower than those used previously to estimate total population size of Northwest Atlantic harp seals.

# RÉSUMÉ

L'obtention d'estimations précises de la fécondité est essentielle si l'on veut estimer la dynamique des populations d'une espèce. On recueille des données sur les taux de gestation des phoques du Groenland de l'Atlantique Nord-Ouest depuis les années 1950. Cependant, la taille de l'échantillon varie fortement et on dispose de peu de données, voire d'aucune, sur la reproduction pour de nombreuses combinaisons d'âge. Dans le but d'obtenir les données requises pour estimer l'abondance totale, nous avons utilisé un estimateur de régression non paramétrique afin d'établir des taux annuels prévus de gestation selon l'âge à l'aide des données recueillies jusqu'en 2007. Le taux de gestation des femelles de 4 ans est demeuré faible (< 10 %) tout au long de la période visée. Les femelles de 5 et de 6 ans affichent un profil similaire; les taux de gestation selon l'âge ont augmenté au départ, au cours des années 1970, mais ont décliné au milieu des années 1980 pour atteindre des niveaux semblables ou inférieurs à ceux observés dans les années 1960. Les taux chez les femelles de 7 ans et plus sont demeurés élevés jusqu'au milieu des années 1980, puis ont décliné pour atteindre les faibles niveaux actuels. Les estimations des taux de reproduction récents sont légèrement inférieures à celles utilisées antérieurement pour estimer la taille de la population totale de phoques du Groenland de l'Atlantique Nord-Ouest.

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#### INTRODUCTION

Monitoring reproduction is an important component in any demographic study of a population (Hedrik 1984). Understanding fecundity, along with mortality, is important for determining the historic population dynamics and predicting future changes. Population regulation through density-dependent changes in fecundity is the result of a complex interaction between intrinsic factors related to changes in population and extrinsic factors involving environmental variability (de Little et al. 2007). However, monitoring such changes is difficult for most species as they require extensive measurements made over long periods. In the absence of such long-term data, changes in fecundity are often incorporated into population models either as a constant or as varying with a density-dependent function (Thomas et al. 2004). The assumption chosen will have a significant impact on the subsequent estimates of abundance and population trajectories (e.g., Thomas et al. 2004).

The harp seal (*Pagophilus groenlandicus*) is an abundant, migratory species distributed throughout most of the North Atlantic. The Northwest Atlantic population summers in Arctic waters of eastern Canada and western Greenland (Sergeant 1991; Stenson and Sjare 1997). In the fall, harp seals migrate southward to overwinter and pup on the pack-ice off the northeast Newfoundland coast or in the Gulf of St. Lawrence. This population is the target of large commercial and subsistence hunts in Canada and Greenland (Stenson 2009), and is managed primarily by quotas on the Canadian commercial hunt which take into account reported catches and other sources of mortality (DFO 2008). These quotas are based upon estimates of population size and predictions of future trends obtained from a population model that incorporates information on removals and annual estimates of age specific reproduction rates with independent estimates of pup production by adjusting the starting population and adult mortality (Hammill and Stenson 2008). Since monitoring of the population is done by estimating pup production, fecundity data are required in order to estimate of total abundance and the impact of hunting.

Unlike most species, we are fortunate to have a long time series of reproductive rates of this population on which to base the population estimates. Female reproductive tracts have been collected from harp seals in Newfoundland and southern Labrador waters since the 1950s, with a more systematic program initiated in the 1980s that continues today (Sjare and Stenson 2010). Bowen et al. (1981) observed that as the population declined during the 1950s and 1960s, the mean age of sexual maturity declined from approximately 6.2 y in 1952 to 4.5 y in 1979, while the pregnancy rate of mature females increased from 85 to 95 %. Bowen et al. (1981) considered it likely that density-dependent mechanisms were involved, but emphasized that sufficient empirical data were still lacking. Sjare and Stenson (2010) evaluated changes in the reproductive parameters of female harp seals up to 2004. They found that pregnancy rates subsequently declined to ~65-70 % by the early 1990s and varied between 45 and 70 % from 2000 to 2004. Concurrently, the mean age at sexual maturity decreased from 5.8 (s.e = 0.02) years in the mid-1950s to 4.1 (s.e. = 0.02) in the late 1970s, increased to 5.5 (s.e. = 0.03) years by the early 1990s, and peaked at 5.7 (s.e. = 0.01) in 1995. From 2000 to 2004, mean age varied from 4.9 (s.e. = 0.01) to 6.0 (s.e. = 0.01) years. Although the direction of changes they observed are consistent with a density dependent response, changes in population size explained relatively little of the variability observed. At the same time, dramatic changes in the Northwest Atlantic ecosystem have occurred suggesting that other ecological or environmental factors have an important influence on carrying capacity (Mclaren et al. 2001; Drinkwater 2004; Siare and Stenson 2010).

Although the data set examined by Sjare and Stenson (2010) is very extensive, few or no samples were available for some age groups and/or years. The objective of this study is to present a method for estimating annual age-specific reproductive rates for northwest Atlantic harp seals using this data set and to extend this time series to 2007. These estimates are required in order to determine the current status of the harp seal population using the model described by Hammill and Stenson (2008)

# MATERIALS AND METHODS

Data to 2004 was taken from Sjare and Stenson (2010). The data and method of collection are summarized here. Since 1980, female reproductive tracts and jaws have been collected from harp seals collected around Newfoundland and southern Labrador, concentrating on a core area along the northeast coast of Newfoundland which is adjacent to key winter and spring feeding habitat (Sergeant 1991; Stenson and Sjare 1997; Fig. 1). Late term pregnancy rates were estimated from seals collected between October and February. Samples were collected by experienced seal hunters and Department of Fisheries and Oceans (DFO) personnel (Fig. 1). We attempted to minimize potential interannual sample biases by ensuring that a core group of hunters from different areas of the province obtained a sample of seals over the entire period. Reproductive tracts were either preserved in 10 % formalin or frozen in the field; in the laboratory, ovaries were cut into 2.0 mm thick serial sections for examination.

Ages were determined to the nearest year by sectioning a lower canine tooth and counting dentine annuli (Fisher 1954; Bowen et al. 1983). Females were considered immature if the ovaries were small and contained only inactive follicles with no *corpus luteum* (CL) or *corpus albicans* (CA) (Fisher 1954; Bowen et al. 1981). If there was evidence of a CL and/or CA in either ovary, the seal was considered mature. Mature females were considered pregnant if the ovary contained a large, fully luteinized CL in one of the ovaries and, since 1990, evidence of a developing fetus and an enlarged, ruggose uterus. Non-pregnant females lacked an active CL, but showed evidence of having ovulated previously (i.e., a CA was present). All seals less than four year of age were considered immature, while seals eight years of age and older were considered fully recruited to the breeding population and grouped together (Sjare and Stenson 2010).

Age-specific sample sizes were highly variable with no reproductive data for many year-age combinations, and in some years the samples are quite small. To fill in data gaps, we assumed that the population pregnancy rates did not vary widely between years and used a non-parametric regression estimator to estimate the expected age-specific pregnancy rates. Assuming that for each age, the number of pregnant seals sampled in year *t* (denoted as  $Y_t$ ) from a total of  $n_t$  was Binomially distributed, with mean  $n_t p_t$  where  $p_t$  was the probability that a seal was pregnant. With no further restrictions on  $p_t$ , the maximum likelihood estimate (mle) of  $p_t$  is  $y_t / n_t$  - the sample proportion of pregnant seals. These problems suggest that some reasonable model restrictions of the  $p_t$ 's are necessary, especially to infer  $p_t$ 's in years not sampled. If the  $p_t$  must be a smooth function of *t*, the amount of smoothness will be determined by the available data. The statistical problem then was to estimate this function or, equivalently, to estimate  $p_t$ . Since it is not possible to estimate  $p_t$  via maximum likelihood without specifying this function more exactly, a non-parametric approach was taken. Local averaging is a commonly used alternative to estimate  $p_t$ . The rationale for local averaging is as follows:

Define an  $\varepsilon$ -neighborhood of observations around a given year t as  $A_t = \{i : | t_i - t | \le \varepsilon\}$ . If  $\varepsilon$  is chosen small enough then it can be assumed that  $p(t_i) = p(t)$  for all i in  $A_t$ . In this case the mle for p(t) is:

(1)

$$\hat{p}(t) = \frac{\sum_{i \in A_t} y_i}{\sum_{i \in A_t} n_i}$$

Only  $y_i$ 's with  $t_i$  values within the  $\varepsilon$  - distance of t have a full contribution to the estimate of p(t). Other  $y_i$ 's have no contribution to the estimate. Another approach is to use a weight function designed so that the contribution of  $y_i$  changes gradually according to the distance between  $t_i$  and t. The weight function W measures the distance between t and  $t_i$ . The size of the neighborhood is determined by a bandwidth, b. The maximum local likelihood estimate is:

(2)

$$\widetilde{p}(t) = \frac{\sum_{i} W\left\{\frac{(t_{i} - t)}{b}\right\} y_{i}}{\sum_{i} W\left\{\frac{(t_{i} - t)}{b}\right\} n_{i}}$$

The Gaussian weight function,  $W(x) \propto \exp(-x^2/2)$ , is used here, although other functions are commonly used. The Gaussian weight function defines elliptical neighborhoods in *t*. As  $b \rightarrow 0$ , the neighborhood includes just  $t_i$ .

The choice of bandwidths is critical in smoothing. A bias-variance trade-off exists in determining the size of the bandwidths. A small bandwidth leads to an estimator with small bias, but large variance (i.e., erratic), while a large bandwidth leads to an estimator with large bias, but small variance (i.e., oversmooth). The data were used to choose a bandwidth, or the amount of smoothness, that minimizes a measure of prediction error. Generalized Cross Validation, a common prediction error measure in kernel smoothing and spline smoothing was used. The amount of smoothness that is useful will depend on age, so bandwidths were selected separately for each age.

Using this approach, reproductive rates were smoothed from 1954 to 2008. Uncertainty in the smoothed estimate was obtained by resampling the annual pregnancy data assuming a binomial distribution and refitting the smoother.

#### RESULTS

Sampling effort has varied throughout the sampling period, with large numbers of animals collected in some years, while in others considerably fewer were obtained (Table 1). Samples from animals aged 8+ years, which consists of animals 8 to 25 years old, exceeded 100 animals in some years. Sample sizes of the remaining age classes show considerable year to year variability. The raw reproductive data are found in Table 1, and the smoothed data are listed in Table 2 (Fig. 2). Fitting the non-parametric regression estimator to the pregnancy rate data shows a slight increase in pregnancy rate of 4 year old animals during 1980-90, but overall only a small proportion (<10 %) of these animals become pregnant (Fig. 2). Among 5 year old

animals, reproductive rates increased from approximately 20 % prior to 1970 to more than 50 % by the late 1970s and, then declined to 20 % by the late 1980s where the central tendency has remained although the raw data show considerable variability. Reproductive rates of 6 year old animals were also highly variable but followed a similar pattern to that seen among 5 year old females with the exception that reproductive rates increased from around 55 % prior to 1970 to 75-80 % by the late 1970s. Reproductive rates have declined since the mid 1980s to 30 % in the current period (Table 2, Fig. 2). Among the 7 and 8 year old animals, pregnancy rates were high throughout the three and a half decades from the mid-1950s until the mid-1980s at an average of 0.8 and 0.9 respectively, then declined in the mid-1980s to current levels of around 0.6 (Table 2, Fig 2).

### DISCUSSION

Reproductive rates remained low for age 4 animals as would be expected for first time breeders. The age 5 and 6 year olds showed a similar pattern with age-specific pregnancy rates increasing during the 1970s to peaks around 1980. By the mid 1980s, however, the proportion of females pregnant declined to levels similar to (age 5) or lower (age 6) than those seen in the 1960s. Older seals (age 7+) did not show an increase during the 1970s but did show a decline in the 1980s at the same time as the 5 and 6 year olds. The rates have remained low since the late 1980s although the raw data are highly variable. This variability may be due to the small sample sizes among the 5-7year olds but this would not explain the inter-annual variation seen among the 8+ class where sample sizes are reasonably large for most years. Even among this group, however, pregnancy rates ranged from 0.45 (2004) to 0.73 (2007) in the past decade. Extending the data from Sjare and Stenson (2010) for 3 more years did not indicate any major changes in reproductive rates from the low levels seen over the past decade.

Hammill and Stenson (2008) used a similar smoothing approach. They extended the smoothed rates to 2005 and then applied the average pregnancy rates of the past 5 years for the 2006-08 period (Fig 3). Incorporating the recent data into the smoothing process has resulted in some important differences, particularly among the older ages. The estimated pregnancy rates for the youngest age group (Age 4) are similar although slightly lower, The results for ages 5 and 6 were very similar with the exception of the last 3 years where Hammill and Stenson (2008) assumed that pregnancy rates had increased. In contrast, our results suggest they remained low or continued to decline. This study indicates that the decline in reproductive rates among the 7+ seals was more extensive than previously estimated for the 1980s and 1990s. However, the adjustment made to the most recent years resulted in estimates similar that those we observed. As a result, the total population estimated using these reproductive rates will likely be higher than those estimated in Hammill and Stenson (2008).

Warren et al (1997) developed a method to group periods of similar reproductive rates using sequential contingency tables identified using Chi square tests. Healey and Stenson (2000) used reproductive rates obtained using this method to estimate total population of harp seals. The general patterns identified using this method, increases in younger seals in the late 1970s and through the mid 1980s followed by a decline in the late 1980s or 1990 for all age groups, are similar to those we observed. However, this earlier method was affected by sample sizes and resulted in knife-edge changes in reproductive rates when sequential block of years were significantly different (Warren et al. 1997). This was a particular problem when the change occurred during a period of years when samples were not available and an arbitrary decision had to made about when the change occurred. Because of these difficulties, we developed the smoothing technique described here to provide annual estimates of age specific pregnancy

rates for incorporation into the population model (e.g., Hammill and Stenson 2008). Recently we been have exploring the use of GAM models to describe changes in reproductive parameters and found similar results (Stenson et al. unpublished data).

The observed changes in pregnancy rates suggests that the population is exhibiting densitydependent changes due either to increasing population densities or declining resources (Eberhardt 1977; Gaillard et al. 2000). The increases seen among 5 and 6 year olds during the mid to late 1970s suggest that this was a good period for young seals. Harp seal populations declined to under 2 million by 1970s but following the implementation of quotas, the population began to increase (Hammill and Stenson 2008). However, with the exception of the youngest age group, all age classes exhibited lower pregnancy rates throughout the 1990s and early 2000s. Although the harp seal population continued to increase in size until the mid 1990s, the decline and subsequent period of variability in rates are also concurrent with major changes in oceanographic conditions and trophic structure of the Northwest Atlantic marine ecosystem. Sjare and Stenson (2010) attempted to correlated changes in mean age of maturity and pregnancy rates with population size. However, they found that that abundance accounted count not explain much of the variation and concluded that other ecological or environmental factors are likely having an important influence. Over the past two decades there have also been highly variable harvests and ice conditions during the whelping period (Stenson 2009; Hammill and Stenson 2008) which may have influenced annual reproductive rates. Therefore, it is not certain that a density-dependent response to changing population size is the primary explanation for these observations. As a result, there is no obvious way of accounting for uncertainty about future changes in pregnancy rates (McLaren 2001).

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	4				5			6			
		No	Preg		No	Preg		No	Preg		
Year	n	Preg	rate	n	Preg	rate	n	Preg	rate		
1954	4	0	0.00	3	1	0.33	3	2	0.67		
1964	11	0	0.00	9	1	0.11	2	1	0.50		
1965	30	1	0.03	44	5	0.11	37	20	0.54		
1966	7	0	0.00	9	1	0.11	17	6	0.35		
1967	10	0	0.00	19	4	0.21	33	20	0.61		
1968	27	0	0.00	19	6	0.32	20	14	0.70		
1969	25	1	0.04	25	4	0.16	16	7	0.44		
1970	13	0	0.00	13	3	0.23	12	6	0.50		
1978	40	1	0.03	38	23	0.61	20	18	0.90		
1979	21	5	0.24	15	8	0.53	5	5	1.00		
1980	2	0	0.00	2	1	0.50	1	1	1.00		
1981	5	1	0.20	4	2	0.50	2	1	0.50		
1982	4	0	0.00	5	2	0.40	1	1	1.00		
1985	4	0	0.00	3	1	0.33	5	2	0.40		
1986	1	1	1.00				2	1	0.50		
1987	12	2	0.17	8	3	0.38	9	7	0.78		
1988	17	2	0.12	6	1	0.17	3	3	1.00		
1989	8	0	0.00	9	1	0.11	6	2	0.33		
1990	8	0	0.00	7	1	0.14	3	1	0.33		
1991	10	0	0.00	11	2	0.18	7	4	0.57		
1992	10	2	0.20	11	3	0.27	9	4	0.44		
1993	11	1	0.09	17	2	0.12	7	0	0.00		
1994	23	1	0.04	16	2	0.13	14	6	0.43		
1995	10	0	0.00	13	6	0.46	4	2	0.50		
1996	8	0	0.00	6	0	0.00	4	1	0.25		
1997	6	0	0.00	4	0	0.00	10	3	0.30		
1998	6	0	0.00	10	3	0.30	9	2	0.22		
1999	6	0	0.00	7	0	0.00	18	4	0.22		
2000	1	0	0.00	9	3	0.33	6	4	0.67		
2001	2	0	0.00				2	2	1.00		
2002	2	0	0.00	4	1	0.25	5	3	0.60		
2003	1	0	0.00	3	2	0.67	2	1	0.50		
2004	1	0	0.00	4	1	0.25	5	1	0.20		
2005	9	1	0.11	9	0	0.00	13	2	0.15		
2006	2	0	0.00								
2007	1	0	0.00	5	0	0.00	3	1	0.33		

Table 1. Age-specific pregnancy rates of female harp seals sampled in Newfoundland and Labrador waters during October to late February from 1954 to 2007. Rates are based on the proportion of pregnant females in a particular age class regardless of maturity status.

Table 1 (Cont'd.)

		7			8+	
		No	Preg			
Year	n	Preg	rate	n	No Preg	Preg rate
1954	16	12	0.75	33	29	0.88
1964	4	3	0.75	25	22	0.88
1965	38	27	0.71	109	96	0.88
1966	11	8	0.73	49	43	0.88
1967	29	28	0.97	123	109	0.89
1968	12	11	0.92	55	48	0.87
1969	28	23	0.82	165	146	0.88
1970	10	9	0.90	107	92	0.86
1978	9	6	0.67	41	35	0.85
1979	9	8	0.89	21	20	0.95
1980				12	10	0.83
1981	7	6	0.86	17	14	0.82
1982	4	3	0.75	3	1	0.33
1985	3	3	1.00	1	1	1.00
1986	1	0	0.00	7	7	1.00
1987	4	4	1.00	24	15	0.63
1988				19	14	0.74
1989	3	2	0.67	22	22	1.00
1990	1	0	0.00	10	6	0.60
1991	3	1	0.33	29	18	0.62
1992	8	6	0.75	32	21	0.66
1993	5	4	0.80	35	17	0.49
1994	7	3	0.43	41	34	0.83
1995	5	2	0.40	24	14	0.58
1996	1	1	1.00	35	24	0.69
1997	2	2	1.00	36	28	0.78
1998	4	2	0.50	35	21	0.60
1999	15	6	0.40	59	37	0.63
2000	5	2	0.40	43	29	0.67
2001	3	0	0.00	39	26	0.67
2002	17	10	0.59	72	39	0.54
2003	3	2	0.67	91	59	0.65
2004				64	29	0.45
2005	7	0	0.00	86	54	0.63
2006				117	56	0.48
2007	2	2	1.00	83	61	0.73

	4			5			6			7			8+		
Year	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV	Mea	ו SD	CV	Mean	SD	CV
1954	0.028	0.017	0.606	0.254	0.200	0.787	0.610	0.217	0.356	0.81	1 0.034	0.042	0.875	0.014	0.016
1955	0.028	0.016	0.579	0.234	0.156	0.667	0.596	0.172	0.290	0.81	1 0.033	0.041	0.875	0.014	0.016
1956	0.028	0.016	0.558	0.211	0.107	0.507	0.579	0.121	0.210	0.81	2 0.032	0.040	0.875	0.013	0.015
1957	0.029	0.016	0.540	0.191	0.068	0.357	0.564	0.081	0.143	0.81	2 0.032	0.039	0.874	0.013	0.015
1958	0.029	0.015	0.524	0.179	0.048	0.269	0.554	0.059	0.107	0.81	2 0.031	0.038	0.874	0.013	0.015
1959	0.030	0.015	0.509	0.172	0.041	0.238	0.548	0.052	0.094	0.81	2 0.031	0.038	0.874	0.013	0.015
1960	0.030	0.015	0.494	0.170	0.039	0.228	0.546	0.049	0.089	0.81	2 0.031	0.038	0.874	0.013	0.015
1961	0.031	0.015	0.479	0.169	0.037	0.220	0.545	0.047	0.086	0.81	2 0.030	0.037	0.873	0.013	0.014
1962	0.032	0.015	0.464	0.170	0.036	0.212	0.544	0.045	0.084	0.81	2 0.030	0.037	0.873	0.013	0.014
1963	0.033	0.015	0.448	0.171	0.035	0.203	0.544	0.044	0.081	0.81	2 0.030	0.037	0.872	0.012	0.014
1964	0.033	0.014	0.431	0.173	0.034	0.195	0.544	0.043	0.079	0.81	2 0.030	0.037	0.872	0.012	0.014
1965	0.035	0.014	0.413	0.175	0.033	0.188	0.545	0.042	0.077	0.81	1 0.030	0.037	0.871	0.012	0.014
1966	0.036	0.014	0.396	0.177	0.032	0.182	0.545	0.041	0.076	0.81	1 0.030	0.037	0.870	0.012	0.014
1967	0.037	0.014	0.378	0.180	0.032	0.179	0.546	0.041	0.075	0.81	0.030	0.037	0.869	0.012	0.014
1968	0.038	0.014	0.360	0.184	0.033	0.177	0.547	0.041	0.076	0.80	9 0.030	0.037	0.868	0.012	0.014
1969	0.040	0.014	0.344	0.191	0.033	0.175	0.550	0.042	0.076	0.80	3 0.030	0.037	0.866	0.012	0.014
1970	0.042	0.014	0.329	0.202	0.034	0.169	0.554	0.043	0.077	0.80	5 0.030	0.037	0.864	0.012	0.014
1971	0.044	0.014	0.316	0.222	0.035	0.156	0.562	0.043	0.077	0.80	4 0.029	0.037	0.862	0.012	0.014
1972	0.046	0.014	0.305	0.255	0.035	0.136	0.578	0.044	0.075	0.80	2 0.029	0.037	0.859	0.012	0.014
1973	0.048	0.014	0.297	0.305	0.036	0.117	0.604	0.043	0.072	0.79	9 0.029	0.037	0.855	0.012	0.014
1974	0.051	0.015	0.290	0.366	0.039	0.108	0.643	0.043	0.067	0.79	5 0.029	0.037	0.851	0.012	0.014
1975	0.053	0.015	0.285	0.426	0.046	0.107	0.691	0.046	0.066	0.79	1 0.029	0.037	0.845	0.012	0.014
1976	0.056	0.016	0.281	0.472	0.051	0.109	0.737	0.051	0.069	0.78	6 0.029	0.037	0.839	0.012	0.014
1977	0.058	0.016	0.277	0.501	0.055	0.111	0.772	0.056	0.073	0.78	0.029	0.038	0.831	0.012	0.014
1978	0.060	0.017	0.274	0.515	0.057	0.111	0.790	0.059	0.075	0.77	3 0.030	0.038	0.821	0.012	0.015
1979	0.062	0.017	0.270	0.519	0.058	0.111	0.793	0.060	0.075	0.76	5 0.030	0.039	0.810	0.012	0.015
1980	0.064	0.017	0.265	0.515	0.057	0.110	0.783	0.058	0.075	0.75	5 0.031	0.040	0.798	0.012	0.015
1981	0.066	0.017	0.261	0.502	0.055	0.110	0.760	0.056	0.074	0.74	5 0.031	0.042	0.785	0.013	0.016
1982	0.067	0.017	0.257	0.477	0.053	0.111	0.725	0.055	0.076	0.73	3 0.032	0.043	0.770	0.013	0.017
1983	0.068	0.017	0.254	0.440	0.050	0.113	0.681	0.056	0.083	0.72	1 0.033	0.045	0.755	0.013	0.018
1984	0.069	0.017	0.252	0.392	0.047	0.121	0.633	0.059	0.093	0.70	3 0.034	0.048	0.741	0.014	0.018
1985	0.069	0.017	0.251	0.339	0.046	0.136	0.587	0.061	0.104	0.69	4 0.035	0.050	0.726	0.014	0.019
1986	0.070	0.018	0.252	0.292	0.045	0.155	0.547	0.061	0.112	0.68	0.036	0.053	0.712	0.014	0.020
1987	0.069	0.018	0.254	0.257	0.045	0.174	0.514	0.060	0.116	0.66	6 0.037	0.056	0.700	0.015	0.021
1988	0.069	0.018	0.257	0.234	0.043	0.185	0.486	0.057	0.118	0.65	3 0.038	0.058	0.689	0.015	0.021

Table 2. Mean, standard deviation (SD) and coefficient of variation (CV) for smoothed age specific reproductive rates from the non-parametric regression. Bandwidths were 0.0417. 0.0204. 0.0466. 0.0526 and 0.0497 for ages 4. 5. 6. 7 and 8+ years, respectively.

	4				5			6						8+		
Year	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV	Mean	, SD	CV	Mean	SD	CV	
1989	0.069	0.018	0.261	0.220	0.042	0.190	0.462	0.055	0.118	0.640	0.039	0.061	0.679	0.015	0.022	
1990	0.068	0.018	0.265	0.212	0.040	0.191	0.440	0.053	0.119	0.627	0.040	0.064	0.670	0.015	0.022	
1991	0.068	0.018	0.270	0.207	0.039	0.190	0.422	0.051	0.121	0.616	0.041	0.067	0.663	0.015	0.022	
1992	0.067	0.018	0.275	0.204	0.038	0.188	0.405	0.050	0.123	0.605	0.042	0.069	0.657	0.015	0.023	
1993	0.066	0.019	0.280	0.202	0.038	0.186	0.391	0.049	0.124	0.595	0.043	0.072	0.651	0.015	0.023	
1994	0.065	0.019	0.285	0.201	0.037	0.184	0.379	0.047	0.125	0.587	0.044	0.074	0.647	0.015	0.023	
1995	0.065	0.019	0.291	0.201	0.037	0.183	0.369	0.047	0.126	0.579	0.044	0.077	0.643	0.015	0.023	
1996	0.064	0.019	0.296	0.202	0.037	0.182	0.361	0.046	0.128	0.571	0.045	0.079	0.639	0.015	0.023	
1997	0.063	0.019	0.302	0.202	0.037	0.184	0.354	0.047	0.132	0.565	0.046	0.081	0.636	0.015	0.024	
1998	0.062	0.019	0.308	0.203	0.038	0.188	0.348	0.047	0.136	0.559	0.046	0.083	0.634	0.015	0.024	
1999	0.061	0.019	0.315	0.203	0.040	0.196	0.343	0.048	0.140	0.554	0.047	0.085	0.632	0.015	0.024	
2000	0.060	0.019	0.323	0.202	0.042	0.206	0.339	0.049	0.145	0.549	0.048	0.087	0.630	0.015	0.024	
2001	0.059	0.020	0.332	0.200	0.044	0.220	0.335	0.051	0.151	0.545	0.049	0.089	0.628	0.015	0.025	
2002	0.058	0.020	0.343	0.198	0.047	0.236	0.331	0.053	0.159	0.541	0.049	0.091	0.627	0.016	0.025	
2003	0.057	0.020	0.356	0.194	0.050	0.257	0.327	0.056	0.170	0.537	0.050	0.093	0.625	0.016	0.025	
2004	0.056	0.021	0.371	0.189	0.053	0.282	0.324	0.059	0.184	0.534	0.051	0.095	0.624	0.016	0.026	
2005	0.055	0.022	0.389	0.184	0.057	0.309	0.320	0.064	0.200	0.531	0.052	0.097	0.623	0.016	0.026	
2006	0.054	0.022	0.410	0.180	0.061	0.338	0.316	0.069	0.218	0.529	0.052	0.099	0.622	0.016	0.026	
2007	0.053	0.023	0.434	0.175	0.065	0.368	0.313	0.074	0.236	0.526	0.053	0.101	0.621	0.017	0.027	
2008	0.053	0.024	0.461	0.171	0.068	0.399	0.311	0.079	0.253	0.524	0.054	0.103	0.620	0.017	0.027	



Figure 1. Winter distribution of Northwest Atlantic harp seals indicating whelping (pupping) and sampling locations for reproductive data. White dots indicate areas where the majority of samples were obtained. Black dots indicate less consistent reproductive sampling areas.











Figure 2. Observed age-specific pregnancy rates (points) and smoothed rates from non-parametric regression.



Figure 3. Smoothed pregnancy rates estimated by Hammill and Stenson (2008, open symbols) and this study (2009, closed symbols).