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Current Reproductive and Maturity Rates of Northwest Atlantic Harp Seals, (*Pagophilus groenlandicus*)

Taux actuels de reproduction et de maturité du phoque du Groenland de l'Atlantique Nord-Ouest (*Pagophilus groenlandicus*)

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ABSTRACT

Obtaining accurate estimates of fecundity are critical for estimating the population dynamics of a species. Annual estimates of late term pregnancy rates, fecundity and mean age of sexual maturity of Northwest Atlantic harp seals were obtained from samples collected off the coast of Newfoundland and Labrador between 1954 and 2008. Pregnancy rates among 3 year olds remained low (<10 %) throughout the time period while those of 4 and 5 year olds initially increased during the 1970s, but declined by the mid 1980s to levels similar to, or lower than, those seen in the 1960s. Pregnancy rates of older seals remained high until the mid 1980s, but then declined to their current low levels. Annual fecundity rates are highly variable. Although they remained high (>85%) until the late 1970s, they subsequently declined and remain low. The increasing trend in mean age of sexual maturity observed since the 1990s has continued. Reproductive rates increased slightly in 2007 and 2008, but are not as high as observed in the 1970s.

RÉSUMÉ

Il est essentiel d'obtenir des estimations précises de la fécondité pour évaluer la dynamique de la population d'une espèce. Des estimés annuels du taux de gestation tardive, de la fécondité et de l'âge moyen de maturité sexuelle des phoques du Groenland de l'Atlantique Nord-Ouest ont été obtenus à partir d'un échantillonnage recueilli sur la côte de Terre-Neuve et du Labrador, entre 1954 et 2008. Le taux de gestation des femelles âgées de trois ans est resté bas (< 10 %) tout au long de cette période. Chez les femelles de quatre et de cinq ans, il a d'abord augmenté dans les années 1970, avant de diminuer au milieu des années 1980, pour ensuite atteindre un niveau équivalent ou inférieur à celui obtenu dans les années 1960. Le taux de gestation des femelles plus âgées est resté élevé jusqu'au milieu des années 1980, puis a diminué jusqu'aux taux bas actuels. Les taux de fécondité annuels varient grandement. Bien qu'ils soient restés élevés (> 85 %) jusqu'à la fin des années 1970, ils ont ensuite diminué et sont restés bas. Par ailleurs, l'âge moyen de maturité sexuelle observé depuis les années 1990 a continué à augmenter. Quant au taux de reproduction, il a légèrement augmenté en 2007 et en 2008, sans toutefois atteindre celui observé dans les années 1970.

INTRODUCTION

Understanding fecundity is critical for determining 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. The harp seal (*Pagophilus groenlandicus*) is an abundant, migratory species distributed throughout most of the North Atlantic. The Northwest Atlantic population summers primarily in the 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 coast of northeast Newfoundland and southern Labrador, 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 reproductive 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 total abundance and the impact of hunting.

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 to 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 (SE = 0.02) years in the mid-1950s to 4.1 (SE = 0.02) in the late 1970s, increased to 5.5 (SE = 0.03) years by the early 1990s, and peaked at 5.7 (SE = 0.01) in 1995. From 2000 to 2004, mean age at sexual maturity varied from 4.9 (SE = 0.01) to 6.0 (SE = 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; Sjare and Stenson 2010). Stenson et al. (2009) extended this dataset with preliminary data from 2004 through 2007; they found that the trends observed by Sjare and Stenson (2010) had continued.

The most recent estimate of harp seal pup production was obtained during surveys carried out in March 2008 (Stenson et al. 2009). Because of irreconcilable differences between visual and photographic surveys of the largest whelping concentration, Stenson et al. (2009) provided two estimates of total pup production. The lowest estimate, 1,076,600 (SE=61,300) was consistent with previous predictions from the population model (Hammill and Stenson 2008) while the higher estimate (1,648,800, SE=118,000) provided a very poor fit to the existing population model (Hammill and Stenson 2009). After examining another survey of this large concentration, Stenson et al. (2010) concluded that pup production was 1,630,300 (SE=110,400). Using

smoothed reproductive rates based on data up to 2007 (Stenson et al. 2009), the population model could fit to a high estimate of pup production only if the reproductive rates of harp seals in 2008 were exceptionally high, i.e. close to the high levels seen in the early 1970s (Hammill and Stenson 2009).

The objective of this study is to complete analyses of the data presented in Stenson et al. (2009) on age specific pregnancy rates from 2004-2007 and to determine if pregnancy rates in 2008 were sufficiently high to account for the large increase in pup production observed during the 2008 survey. We also extend the analysis of Sjare and Stenson (2010) to determine current fecundity rates and mean age at sexual maturity for northwest Atlantic harp seals.

MATERIALS AND METHODS

Data to 2003 were taken from Sjare and Stenson (2010). The data for 2004 were updated and incorporated into our analyses. The data and methods of collection are summarized in Stenson et al. 2009. Female reproductive tracts and jaws were collected from harp seals collected around Newfoundland and southern Labrador since 1979. Sampling has focused upon 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). Samples were collected by experienced seal hunters and Department of Fisheries and Oceans (DFO) personnel. 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 1985, the presence of a foetus. Mature non-pregnant females lacked an active CL, but showed evidence of having ovulated previously (i.e., a CA was present). As in previous studies, all seals less than three years of age were considered immature (Sjare and Stenson 2010).

The reproductive data for harp seals dating from 1980 – 2008 were thoroughly checked and cleaned of errors. For seals that lacked a developing foetus but had a CL \geq 13 mm or CA \geq 12 mm, a rugose uterus and a large uterine horn width difference (\sim 15.0 mm), it was assumed that pupping had recently occurred. For seals collected prior to February 1st, it was further assumed that those pups did not survive. For seals collected February 1st onward, it was assumed that there was a high probability that these pups contributed to the population that year. These situations were rare and therefore had a negligible effect on overall pregnancy rates.

Fecundity rates, defined as the proportion of mature females that are pregnant, and age specific pregnancy rates were calculated as per Sjare and Stenson (2010). Late term pregnancy and fecundity rates were estimated from seals collected between October and February. As in Sjare and Stenson (2010), mean and variance of age at sexual maturity (MAM) were calculated following DeMaster (1978; 1984). MAM was based on samples collected from April through February (i.e. all months but March). Estimates of MAM prior to 1980 were taken from Sjare and

Stenson (2010). The data from 1980 onward were reanalysed. As well, data from 2001 to 2008 were combined in groups of 2 years in order to obtain adequate sample sizes for the analyses.

RESULTS

Age specific pregnancy rates

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). With the exception of some years in the mid 1980s when sample sizes were very small, samples from animals 8 years and older have generally been greater than 25. Sample sizes for older seals have improved in recent years. For younger animals, however, sample sizes are quite small in most years throughout the time series.

The additional data presented here are consistent with the trends described by Sjare and Stenson (2010). Generally, pregnancy rates for 3 year olds were very low with few animals being pregnant. Among the 4 and 5 year olds, reproductive rates were higher during the late 1970s and early 1980s than in earlier years. Since the mid 1980s pregnancy rates have declined to the lowest in the time series. Pregnancy rates for 6 year olds were low (< 67%) since the mid 1990s when compared with earlier years when rates averaged around 80%. 7 year old seals also had relatively low pregnancy rates from 2002-2008 when compared with earlier years, with the lowest year on record being 2005 (17%). Among the 8+ animals, pregnancy rates were high (80–90%) until the mid 1980s, but then declined. Since then, pregnancy rates have fluctuated greatly being as low as 38% in 2004 and averaging around 60%. In 2007 and 2008, however, the rates were the highest since 1990 (76.8 and 77.2%, respectively).

Fecundity rates

Until the late 1970s, more than 85% of the mature females were pregnant each year. Since then fecundity rates have been highly variable, but show a declining trend (Table 2, Fig. 2). The lowest rate in the time series occurred in 2004 (40%) while the rates in 2007 and 2008 (75.3 and 73.8%, respectively) were the highest seen in 10 years.

Mean age of sexual maturity (MAM)

The estimates of MAM from 1980 through 2000 that we obtained were similar to those presented in Sjare and Stenson (2010). There were slight differences in estimated values for MAM, generally less than 0.1 year, and increases in the reported sample sizes.

From 1954 to 1976, the MAM averaged 5.3 years (Table 3, Fig. 3). Between 1978 and 1987, however, it declined to an average of 4.6 years of age. Throughout the 1990s, MAM remained fairly constant around 5.6 years. With the exception of 2000, MAM increased during the early 2000s reaching a time-series high of 6.1 (var = 0.08) years in 2005-06. In 2007-08, the estimated MAM declined to 5.3 (var = 0.10) years, although sample sizes in the important age classes (3-8 years of age) were small.

DISCUSSION

The highly variable, but generally declining reproductive rates observed by Sjare and Stenson (2010) have continued since 2004. Adding additional samples collected in 2004 and extending the data to 2008 did not result in any change in our perception of the trends reported previously. Although small sample sizes among young animals made it difficult to determine precisely what their reproductive rates now are, mean age of sexual maturity continued to increase to more than 6 years of age. These data suggest that the population is continuing to exhibit density-dependent changes due either to increasing population densities or declining resources (Eberhardt 1977; Gaillard et al. 2000). Sjare and Stenson (2010) attempted to correlate changes in mean age of maturity with population size, but found that population size could not explain much of the variation over the entire time series. They concluded that other ecological or environmental factors are also impacting the population. New estimates of abundance will be available once the results of the 2008 pup production survey are confirmed (Hammill and Stenson 2011). Once available, the data should be reanalyzed to determine if there is still evidence of an environmental impact on reproductive rates or if changes in abundance can explain more of the variation.

Previous attempts to estimate total harp seal abundance (e.g. Hammill and Stenson 2009) used a modeling approach that incorporated removals and reproductive rates that smoothed the interannual variability in pregnancy rates (Hammill and Stenson 2008, 2009, Stenson et al. 2009). Using this approach Hammill and Stenson (2009) were unable to explain the large increase in pup production observed in 2008 (Stenson et al. 2011). They could, however, account for this higher estimate if they assumed that there was a dramatic increase in the 2008 pregnancy rates to those seen during the 1970s and early 1980s. We found that although pregnancy rates in 2007 and 2008 were higher than those of the previous 10 years, they were still lower than those seen earlier and were not high enough to account for the 2008 pup production if the smoothed rates were used prior to this (Hammill and Stenson 2009). Including these recent data into new estimates of the smoothed rates did not improve the fit of the model to the 2008 pup production estimate. This suggests that we should reconsider how we incorporate the reproductive data into the population model and consider using the annual estimates as more accurate indicators of interannual variability in reproductive performance (Hammill and Stenson 2011).

Even though the data show a clear overall trend in declining reproductive rates, the interannual variation in the data is extremely high, particularly since the early 1990s. While the general decline may be a reflection of density dependent processes associated with increased population size, the cause of the large interannual variability is less clear. Previously, we assumed that the variability was due, to some extent, to sampling error and therefore smoothed the data to provide a better estimate of trends in reproductive rates (e.g. Stenson et al. 2009). However, it is possible that the variability around the trend may be real and reflect annual changes in the environment or resources that will affect fecundity in a particular year.

Because the opportunistic nature of sampling, there were interannual differences in the number and locations of samples. For example, sample sizes were quite low in the mid 1980s, and again in the early 2000s, while the proportion of samples obtained from different areas varied with year. Preliminary analyses of changes in the annual fecundity rate (i.e. proportion of mature females pregnant) using logistic regressions with both binomial and quasibinomial error structures indicate that there is clearly a significant change over time (Koen-Alonso unpublished data). However, the region from where the samples were obtained and the sample sizes, also appear to have some impact on observed fecundity rates. The age of the animal was not

significant in any of the models. Although the effects of zone and sample size are not dismissible, the main driver of changes in annual fecundity rate appears to be associated with changes over time. The influence of sample size and/or location may also be affected by the year trend since the variability in sampling was relatively small in the earlier years of the time series. These analyses suggest that while sample size and location must be considered, the data do reflect actual changes in annual fecundity rates that are not accounted for by the trend alone. This will now allow us to explore how extrinsic (e.g. food availability, ice coverage; NAO index) and/or intrinsic factors (e.g. relationship between pregnancy in one year vs. the next; years of high pup mortality, etc.) may be affecting fecundity of northwest Atlantic harp seals.

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Table 1. Age specific pregnancy rates of female harp seals sampled in Newfoundland and Labrador waters during October to late February from 1954 to 2008. Rates are based on the proportion of pregnant females in a particular age class regardless of maturity status.

Year	3			4			N	5	
	n	No Preg	Preg rate	n	No Preg	Preg rate		No Preg	Preg rate
1954	4	0	0	3	1	0.333	3	2	0.667
1964	11	0	0	9	1	0.111	2	1	0.500
1965	30	1	0.033	44	5	0.114	37	20	0.541
1966	7	0	0	9	1	0.111	17	6	0.353
1967	10	0	0	19	4	0.211	33	20	0.606
1968	27	0	0	19	6	0.316	20	14	0.700
1969	25	1	0.040	25	4	0.160	16	7	0.438
1970	13	0	0	13	3	0.231	12	6	0.500
1978	40	1	0.025	38	23	0.605	20	18	0.900
1979	21	5	0.238	15	8	0.533	5	5	1.000
1980	2		0	2	1	0.500	1	1	1.000
1981	5	1	0.200	4	3	0.750	2	1	0.500
1982	4		0	5	2	0.400	1	1	1.000
1985	4		0	3	1	0.333	5	2	0.400
1986	1	1	1.000			-	2	1	0.500
1987	12	2	0.167	8	3	0.375	9	7	0.778
1988	17	2	0.118	6	1	0.167	3	3	1.000
1989	8		0	9		0	6	2	0.333
1990	8		0	7	1	0.143	3	1	0.333
1991	10		0	11	2	0.182	7	4	0.571
1992	10	2	0.200	11	3	0.273	9	4	0.444
1993	11	1	0.091	17	2	0.118	7		0
1994	23	1	0.043	16	2	0.125	14	6	0.429
1995	10		0	13	6	0.462	4	2	0.500
1996	8		0	6		0	4	1	0.250
1997	6		0	4		0	10	3	0.300
1998	6		0	10	3	0.300	9	2	0.222
1999	6		0	7		0	18	4	0.222
2000	1		0	9	3	0.333	6	4	0.667
2001	2		0			-	2	2	1.000
2002	2		0	4	1	0.250	5	3	0.600
2003	1		0	3	2	0.667	2	1	0.500
2004	2		0	5		0	5	1	0.200
2005	9	1	0.111	9		0	13	2	0.154
2006	2		0			-			-
2007	1		0	5		0	3	1	0.333
2008	6		0	3		0	2		0

Table 1 (Cont'd.)

Year	6			7			8+		
	n	No Preg	Preg rate	n	No Preg	Preg rate	n	No Preg	Preg rate
1954	16	12	0.750	4	3	0.750	29	26	0.897
1964	4	3	0.750	5	5	1.000	20	17	0.850
1965	38	27	0.711	33	28	0.848	76	68	0.895
1966	11	8	0.727	8	7	0.875	41	36	0.878
1967	29	28	0.966	23	20	0.870	100	89	0.890
1968	12	11	0.917	11	9	0.818	44	39	0.886
1969	28	23	0.821	29	27	0.931	136	119	0.875
1970	10	9	0.900	19	18	0.947	88	74	0.841
1978	9	6	0.667	10	7	0.700	31	28	0.903
1979	9	8	0.889	4	4	1.000	17	16	0.941
1980			-	2	2	1.000	10	7	0.700
1981	7	6	0.857			-	17	14	0.824
1982	4	3	0.750			-	3	1	0.333
1985	3	3	1.000			-	1	1	1.000
1986	1		0	1	1	1.000	6	6	1.000
1987	4	4	1.000	1	1	1.000	23	14	0.609
1988			-	3	2	0.667	16	12	0.750
1989	3	2	0.667	2	2	1.000	20	20	1.000
1990	1		0			-	10	6	0.600
1991	3	1	0.333	3	1	0.333	26	17	0.654
1992	8	6	0.750	2	2	1.000	30	19	0.633
1993	5	4	0.800	3	2	0.667	32	15	0.469
1994	7	3	0.429	5	5	1.000	36	29	0.806
1995	5	2	0.400			-	24	14	0.583
1996	1	1	1.000			-	35	24	0.686
1997	2	2	1.000	2	1	0.500	34	26	0.765
1998	4	2	0.500	9	6	0.667	27	16	0.593
1999	15	6	0.400	9	7	0.778	50	30	0.600
2000	5	2	0.400	6	3	0.500	37	26	0.703
2001	3		0	3	3	1.000	36	23	0.639
2002	17	10	0.588	7	4	0.571	65	36	0.554
2003	3	2	0.667	4	2	0.500	87	57	0.655
2004	1		0	8	5	0.625	68	26	0.382
2005	7		0	6	1	0.167	80	54	0.675
2006			-	5	3	0.600	114	64	0.561
2007	2	2	1.000	2	1	0.500	82	63	0.768
2008			-	4	1	0.250	57	44	0.772

Table 2: Annual late-term fecundity (# females pregnant / # females mature) rates of female harp seals sampled in Newfoundland and Labrador waters from October through February, 1954 – 2008.

Year	# mature females	Fecundity rate
1954	51	0.863
1964	32	0.844
1965	161	0.925
1966	59	0.983
1967	163	0.988
1968	85	0.929
1969	187	0.968
1970	116	0.948
1978	88	0.943
1979	51	0.941
1980	14	0.786
1981	29	0.862
1982	9	0.778
1985	10	0.700
1986	10	0.900
1987	44	0.705
1988	26	0.769
1989	31	0.839
1990	14	0.571
1991	36	0.694
1992	55	0.655
1993	47	0.511
1994	60	0.767
1995	36	0.667
1996	38	0.684
1997	42	0.762
1998	44	0.659
1999	80	0.588
2000	54	0.704
2001	42	0.667
2002	93	0.581
2003	95	0.674
2004	80	0.400
2005	95	0.611
2006	119	0.563
2007	89	0.753
2008	61	0.738

Table 3 Mean age of sexual maturity (MAM) for harp seals sampled in Newfoundland and Labrador waters from April to late February, 1954-2008. Data prior to 1980 taken from Sjare and Stenson (2010).

Year	<i>n</i>	Mean	Variance
1954	211	5.8	0.02
1962	89	4.9	0.07
1964	75	4.8	0.02
1965	283	5.6	0.02
1966	233	5.8	0.02
1967	235	5.1	0.02
1968	169	5.2	0.03
1969	284	5.6	0.03
1970	291	5.1	0.03
1976	155	5.2	0.12
1978	193	4.7	0.02
1979	131	4.1	0.03
1980	39	4.5	0.25
1981	202	4.7	0.06
1982	124	4.7	0.01
1983	192	4.6	0.01
1984/1985	150	4.5	0.04
1986/1987	250	4.6	0.04
1988	118	5.6	0.18
1989/1990	181	5.4	0.09
1991	125	5.6	0.21
1992	399	5.4	0.02
1993	315	5.5	0.06
1994	275	5.6	0.08
1995	282	5.6	0.04
1996	268	5.6	0.06
1997	354	5.6	0.02
1998	486	5.5	0.03
1999	277	5.5	0.05
2000	583	4.9	0.03
2001/2002	512	5.4	0.07
2003/2004	769	5.8	0.07
2005/2006	604	6.1	0.08
2007/2008	415	5.3	0.10

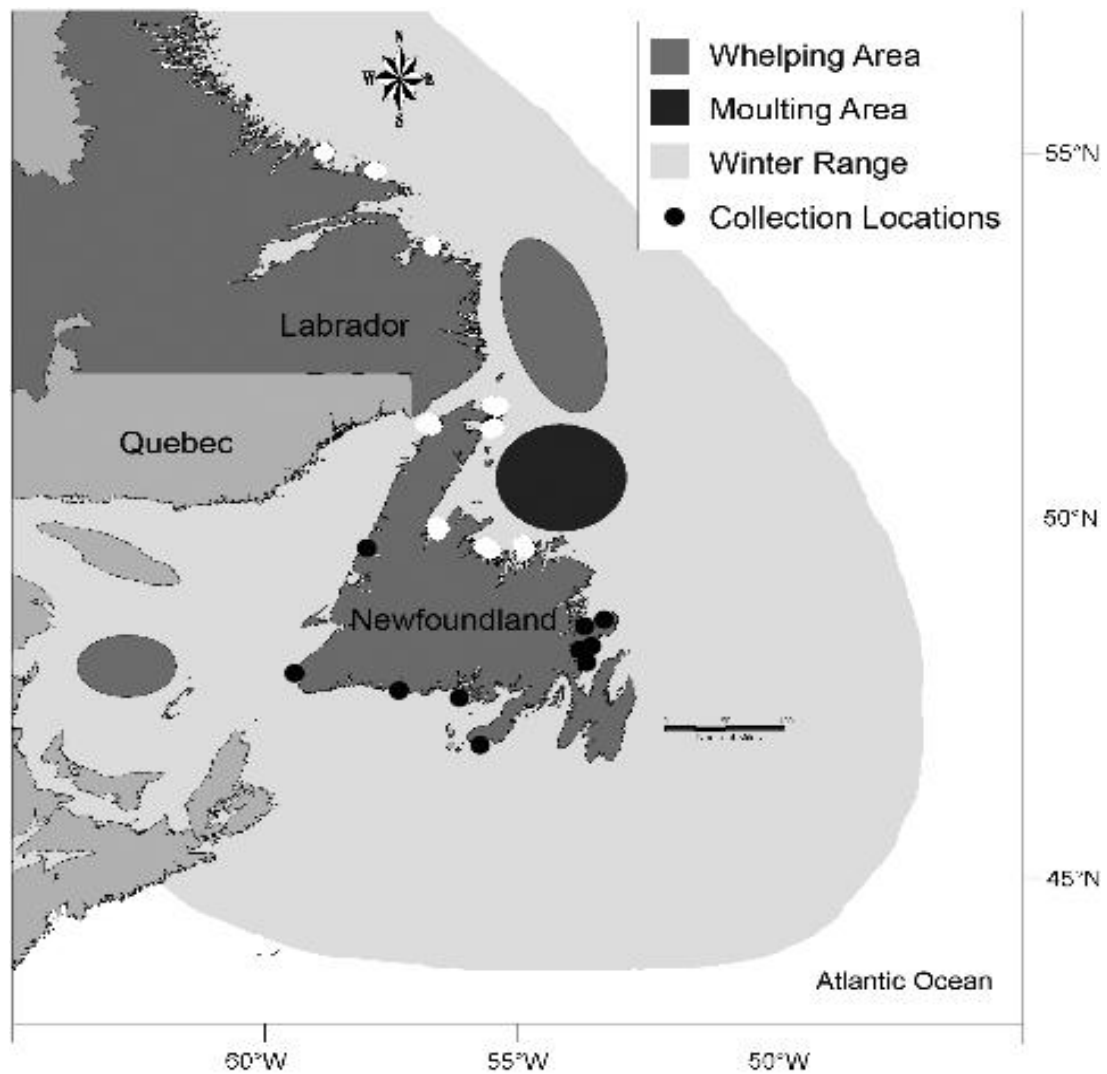


Figure 1. Winter distribution of Northwest Atlantic harp seals indicating whelping (pupping) and sampling locations for reproductive data. White dots indicate areas where the majority of samples were obtained. Black dots indicate less consistent reproductive sampling areas.

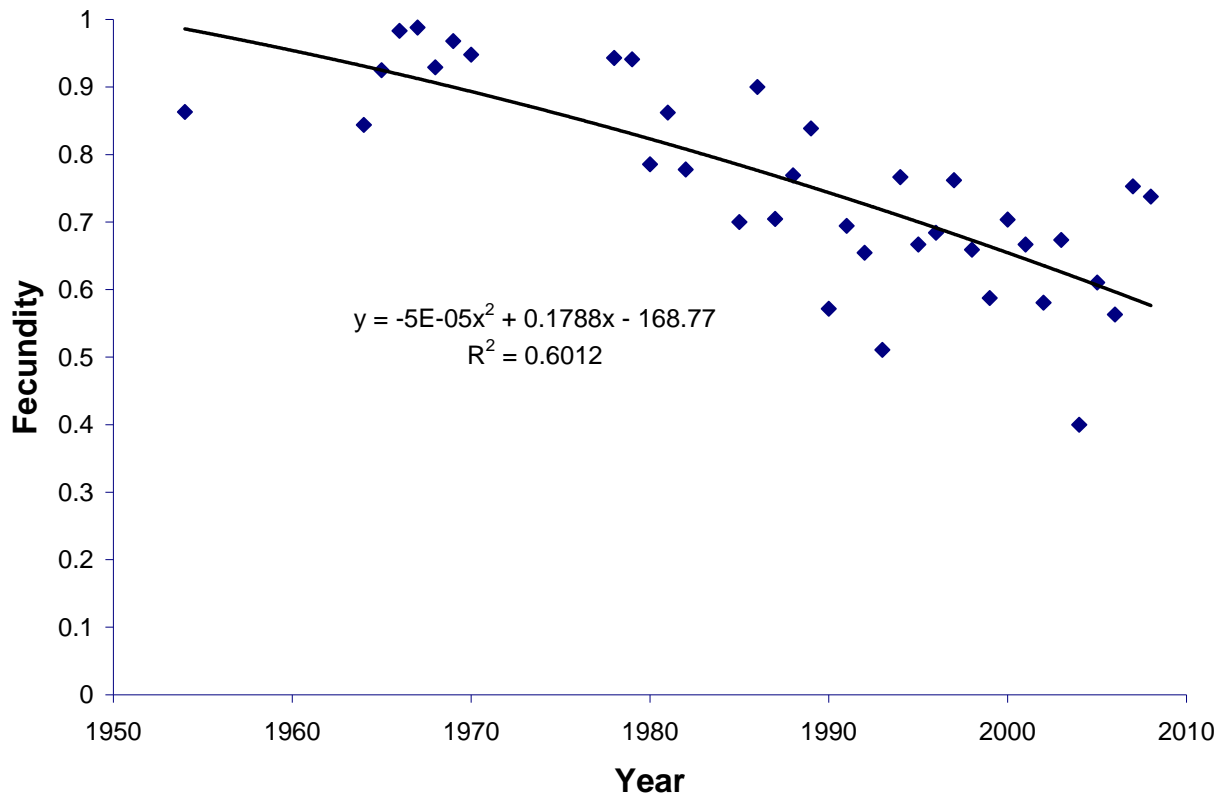


Figure 2 Relationship between year and annual late-term pregnancy rates of mature females (i.e. fecundity) sampled from October to late February from 1954 to 2008.

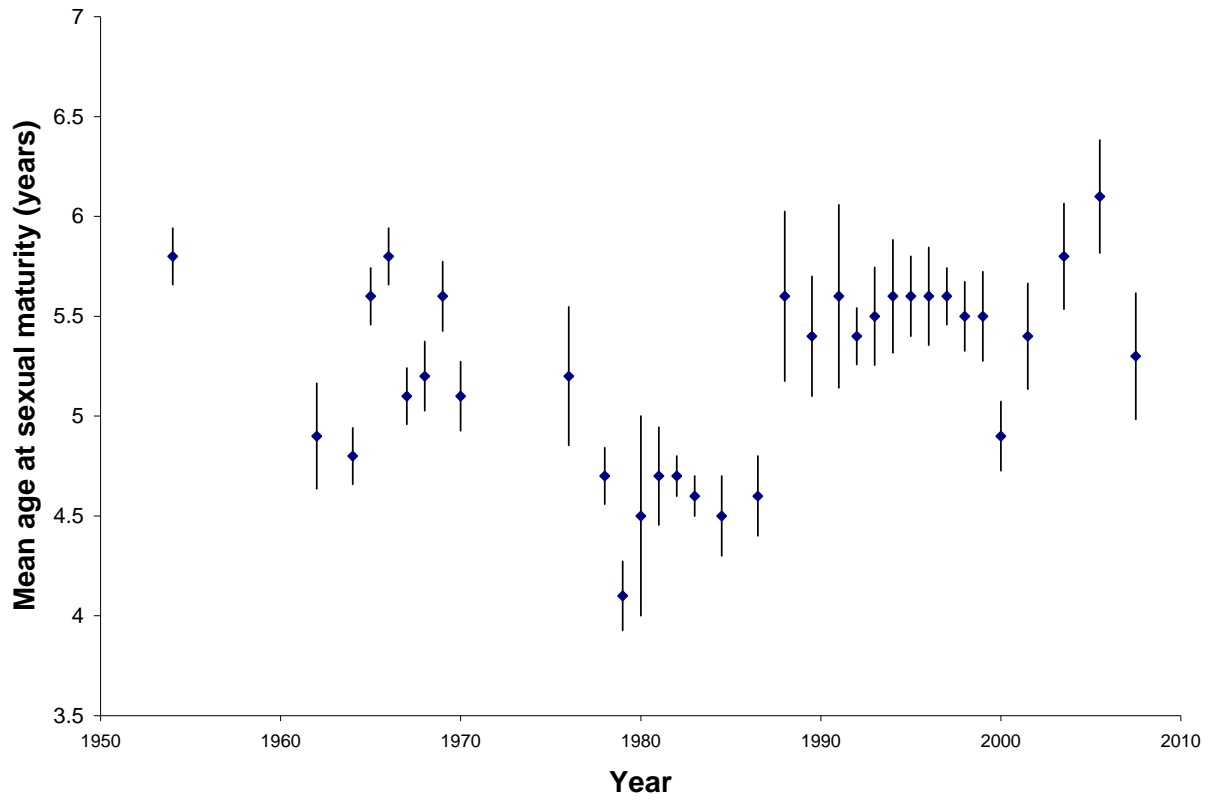


Figure 3. Mean age of sexual maturity (± 1 SD) in female harp seals, 1952-2008.