

# Pup production and population trends of the grey seal (*Halichoerus grypus*) in the Gulf of St. Lawrence

M.O. Hammill, G.B. Stenson, R.A. Myers, and W.T. Stobo

**Abstract:** Grey seal (*Halichoerus grypus*) pup production of the Gulf of St. Lawrence component of the Northwest Atlantic grey seal population was determined for the 1984–1986 and 1989–1990 periods using mark–recapture methods. Pup production estimates based on recaptures from shot samples from Anticosti Island ranged from 5436 (SE = 672) to 6955 (SE = 1183) for 1984–1986. An independent estimate for 1984–1986, based on animals captured on Sable Island, was 7431 (SE = 1414) to 8633 (SE = 2827). Mark–recapture estimates of pup production for 1989 and 1990 from shot samples collected from Anticosti Island were 8825 (SE = 3164) and 9156 (SE = 2652), respectively. The estimates based on animals captured on Sable Island varied from 7295 (SE = 2118) to 8116 (SE = 846) for 1989–1990. Both the Anticosti Island and Sable Island recovery samples underestimate 1989 pup production due to hunting which removed 1612 pups from the population before they could disperse. The Gulf component of the Northwest Atlantic grey seal population is increasing at an annual rate of 7.4% (SE = 2.2).

**Résumé :** La production de jeunes phoques gris (*Halichoerus grypus*) dans le golfe du Saint-Laurent a été estimée pour les périodes de 1984–1986 et 1989–1990 à l'aide de la méthode de marquage–recapture. La production de jeunes estimée par marquage–recapture, basée sur la chasse d'animaux à l'île d'Anticosti, s'étendait de 5436 (ET = 672) à 6955 (ET = 1183) pour la période de 1984 à 1986. Une estimation basée sur la capture d'animaux vivants à l'île de Sable a évalué une production de jeunes variant de 7431 (ET = 1414) à 8633 (ET = 2827) pour la période de 1984 à 1986. Les estimations de production de jeunes par marquage–recapture, basées sur des animaux tués à l'île d'Anticosti, étaient respectivement de 8825 (ET = 3164) et de 9156 (ET = 2652) pour 1989 et 1990. Les estimations basées sur la capture d'animaux vivants à l'île de Sable variaient de 7295 (ET = 2118) à 8116 (ET = 846) pour 1989 à 1990. Les échantillons de recapture de l'île d'Anticosti et de l'île de Sable sous-estiment la production de jeunes en 1989 puisque 1 612 jeunes furent retirés de la population avant que celle-ci se disperse. La portion de la population de phoques gris ne se reproduisant pas à l'île de Sable croît à un taux annuel de 7,4% (ET = 2,2).

## Introduction

Information on abundance is fundamental to addressing many management issues, including harvesting strategies and the control of pests and conservation of species. Over the last 50 years, a reduction in harvesting activity has permitted many pinniped populations to increase. This situation has raised concerns that seals may have an impact on commercial fisheries through damage to fishing gear, transmission of parasites, and competition with fishers (Malouf 1986).

The grey seal (*Halichoerus grypus*) is distributed on both sides of the North Atlantic Ocean. Three populations, separated both geographically and genetically, are generally recognized: the

Northeast Atlantic, Northwest Atlantic, and Baltic Sea populations (Davies 1957; Boskovic et al. 1996). During the 1960s, the Northwest Atlantic grey seal population was thought to number around 5000 animals (Mansfield 1966). Since then the population has increased (Thompson and Mansfield 1990). In the Northwest Atlantic, there are two large breeding concentrations of grey seals. The most intensively studied group whelps on Sable Island, 200 km off the Nova Scotia coast (Mansfield 1966; Mansfield and Beck 1977), while a second concentration breeds on the pack ice in the southern Gulf of St. Lawrence (Mansfield 1966). Other small groups (<500) whelp on small islands in the Gulf of St. Lawrence and along the Nova Scotia Eastern Shore (Mansfield and Beck 1977) (Fig. 1).

Pup production on Sable Island is well documented as a result of a program of complete tagging conducted between 1977 and 1990. Pup production in 1989, the last year for which there are published estimates, was 9712 animals (Stobo and Zwanenburg 1990). This component of the grey seal population is increasing at an annual rate of 12.6% (Stobo and Zwanenburg 1990). Mohn and Bowen (1996) modelled the changes in population size of the Sable Island component and estimated a total population of 85 300 (78 000 – 95 000) grey seals in 1994.

Less is known about grey seal pup production in other areas, most of which are born in the Gulf of St. Lawrence, due to logistical difficulties associated with working on the drifting

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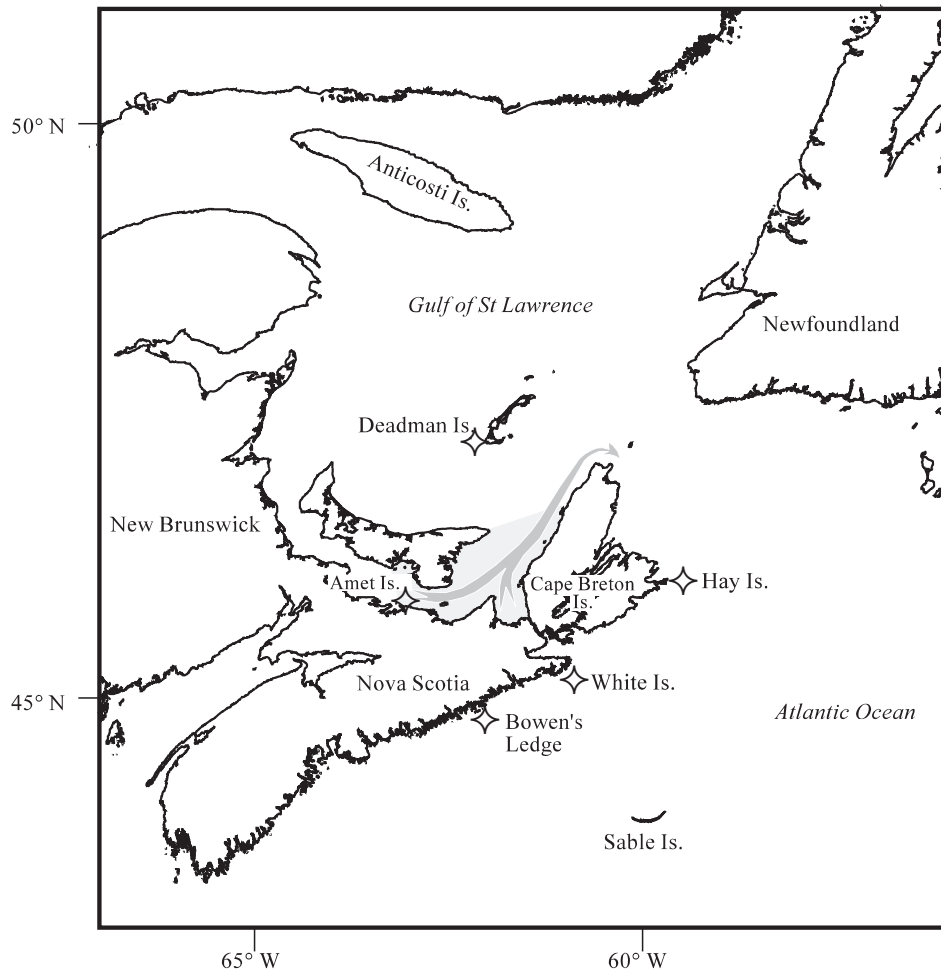
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**Fig. 1.** Location of whelping patches on the ice in the southern Gulf of St. Lawrence and general direction of ice drift. Pupping colonies in the Gulf and along the Nova Scotia Eastern Shore are denoted by diamonds.



pack ice. Mark-recapture estimates from 1984 to 1986 range from a low of 5295, based on the recovery of tags in scientific collections from Anticosti Island, to a high of 11 694 animals, based on the resighting of tagged and untagged pups from the Gulf that had migrated to Sable Island during the spring (Stobo and Zwanenberg 1990). The wide range in these estimates suggests that several assumptions of the Petersen estimator were violated and it was concluded that the true population size likely lay in between the two estimates (Stobo and Zwanenberg 1990). The population trajectories of the Sable Island and Gulf components are also likely to be quite different owing to a combination of higher pup mortality rates on the unstable pack ice, a government cull on the whelping patch (1967–1984), and a bounty system (Zwanenburg and Bowen 1990) throughout the Gulf and along the Eastern Shore (1976–1992)

Here, we use seal pups tagged in the southern Gulf of St. Lawrence and along the Eastern Shore and subsequently resighted or recaptured on Sable Island or on Anticosti Island to estimate non-Sable Island grey seal pup production. Since the majority of these animals are born in the Gulf of St. Lawrence, we refer to it as the Gulf component of the population. We assume random mixing of tags between tagging sites and recapture sites and use alternative methods when evidence is

found of nonrandom mixing. We also present estimates of 1989 and 1990 pup production and examine changes in population size over time.

## Materials and methods

### Study area

In the Gulf, the majority of pups are born on the pack-ice in Northumberland Strait and St. George's Bay. The specific location of whelping animals is dictated by the availability of suitable ice. Grey seals appear to prefer rafted pack ice 40–80 cm thick (M.O. Hammill, personal observation). Ice formation begins during the middle of December along the New Brunswick coast and in Northumberland Strait. This ice drifts towards the east and northwards along the west coast of Cape Breton exiting via Cabot Strait into the Atlantic Ocean (Markham 1980). Ice stability depends on local wind conditions. Although the prevailing winds are westerly (Markham 1980), sudden shifts to the northwest will move ice into St. George's Bay, while changes to southerly winds can clear St. George's Bay overnight (M.O. Hammill, personal observation).

Smaller pupping colonies are found on small islands in the Gulf and along the Nova Scotia Eastern Shore (Mansfield and Beck 1977) (Fig. 1). Pupping on the small islands in the Gulf and along the Eastern Shore begins in late December, while pupping on the ice begins in early January. The buildup in number of births occurs rapidly, with

65% of the births occurring by 23 January. However, the season of births is prolonged, with newborn pups still appearing on the ice in early February.

**Mark-recapture experiments**

Grey seal pups were marked during December–February with a uniquely numbered flipper tag (Dalton Supplies Ltd, Nettlebed, Henley-on-Thames RG9 5AB, England) prior to weaning. On Sable Island, virtually all pups born on the island were tagged between 1977 and 1990. Along the Eastern Shore, both culling and tagging of animals occurred. Pups were culled in 1984 on Camp ( $N = 50$ ) and Basque islands ( $N = 30$ ), while another 14 pups were tagged on Bowens Ledge. A total of 125, 144, and 172 pups were tagged along the Eastern Shore in 1985, 1986, and 1989, respectively. In the Gulf, pups were tagged during 1984 ( $N = 1409$ ), 1985 ( $N = 2118$ ), 1986 ( $N = 1537$ ), and 1989 ( $N = 2551$ ). However, in 1989, late ice breakup and good hunting conditions resulted in 1612 pups being killed in the Gulf before May, including 718 tagged pups. This reduced the effective number of tags in 1989 to 1833. In 1990, only pups in the Gulf were tagged ( $N = 2219$ ). Pups were marked with a single numbered tag in 1984 and 1990, double tagged in 1986, and single or double tagged in 1985 and 1989.

Recaptures were obtained from Anticosti Island (by shooting) and from Sable Island (by live capture and release). Recaptures from these two sites were analysed separately. For all recaptures, animals were examined for the presence of a tag or evidence of tag loss. Tags recovered from animals born on Sable Island were excluded from the analyses because it was assumed that all animals were tagged.

During the summer, large numbers of grey seals can be found around Anticosti Island in the northern Gulf (Clay and Nielsen 1985). Recaptures from this area were from shot samples obtained as part of scientific collection programs undertaken on Anticosti Island during June–September 1986, 1987, 1988, and 1992. Lower jaws were removed from shot samples and the age was determined for animals that did not have tags by three readings of a cross section of a lower canine tooth (Mansfield 1991).

Some pups born in the Gulf remain with the pack ice as it moves through Cabot Strait into the Atlantic Ocean, where it drifts in a southeasterly direction along the coast of Nova Scotia. Throughout the spring, many of these young-of-the-year (YOY) animals from the Gulf end up on Sable Island. To obtain a second estimate of the population, pups were captured on Sable Island during the months of March–October 1984–1986 (Stobo and Zwanenburg 1990) and May–June 1989 and 1990, checked for tags, and released. In association with this experiment, a sample of yearlings was also shot on Sable Island during January–February 1986. In late January – early February 1990, randomly allocated transects were completed through the weaned pup concentrations on Sable Island. These surveys indicated that <2% of the Sable Island born pups were untagged. Consequently, the number of animals without tags was reduced by 2% to account for Sable Island animals that were missed during tagging, and the remaining untagged animals were assumed to have been born in the Gulf or in one of the small colonies along the Eastern Shore.

**Pup production estimation**

Pup production was determined using the program Stratified Population Analysis System (SPAS) (Arnason et al. 1996). Both mark and recapture phases were stratified. The marking phase was stratified into three strata: tags applied in the first half of the marking season (early), tags applied in the second half of the marking season (late), and tags applied along the Eastern Shore. The recovery phase was also stratified by month or year of tag recovery.

Pup production ( $N$ ) was estimated using the modified Petersen estimator (Chapman 1951):

$$N = \frac{(M + 1)(n + 1)}{(m + 1)} - 1$$

where  $M$  is the total number of animals tagged,  $n$  is the total number of animals recaptured, and  $m$  is the total number of tagged animals recaptured. The variance ( $\text{Var}(N)$ ) and standard error of the estimate  $S(N)$  were calculated from

$$S(N) = \sqrt{\text{VAR}(N)} = \frac{(M + 1)(n + 1)(M - m)(n - m)}{(m + 1)^2(m + 2)}$$

Arnason et al. (1991) found that the usual method of calculating 95% confidence intervals  $N \pm 1.96 \cdot S(N)$  was not adequate for small sample sizes of  $m$  and suggested the alternative:

$$\begin{aligned} T &= M^{-1/3} \\ S(T) &= T \cdot S(N) / (3N) \\ (T_L, T_U) &= T \pm 1.96S(T) \\ (N_L, N_U) &= 1/T_U^3, 1/T_L^3 \end{aligned}$$

where  $M$  is the total number of animals marked,  $N$  is the estimated pup production, and  $N_L$  and  $N_U$  are the 95% confidence limit estimates of pup production.

When recoveries are pooled from several sampling periods, the Petersen estimator is called the pooled Petersen estimator (PPE). An important assumption of this method is that all animals have the same probability of capture across all recovery strata. The validity of pooling the data was tested using chi-square tests to determine if the proportion of each initial stratum marked is constant across all capture stratum (equal proportions test) and to determine if the probability of recapturing an animal was independent of its stratum of origin (complete mixing test). A significant chi-square for either of these tests indicates that pooling of data may not be valid and hence the estimate may be biased (Arnason et al. 1996). However, the validity of chi-square tests is limited when test cells have an expected frequency of <5 (Siegel 1956). Also, Arnason et al. (1996) cautioned that significant values in either test may not always indicate that partial or complete pooling of data is invalid and suggested that if pooling does not produce large changes in the estimates (>1 SE), then pooling may still be valid. When the hypotheses for complete mixing and equal proportion of tags in the recovery samples were rejected, we examined the possibility of estimating pup production using the Darroch method. This model assumes that the probability of capture is constant within strata, but permits capture probabilities to vary between strata (Darroch 1961). SPAS provides solutions to determine pup production using the Darroch estimator based on a maximum likelihood method (ML Darroch) developed by Plante (1990) and also tests for significant differences between the observed and expected recaptures from the fitted model using a goodness of fit test ( $G^2$  test). If this test was also significant, then we concluded that no unbiased estimate was possible.

The rate of population increase was estimated by fitting a non-linear regression model by least squares to the estimates of pup production obtained from mark-recapture data using the equation  $N_t = N_0 e^{rt}$  (Caughley 1977) where  $N_0$  is initial population size,  $r$  is the observed rate of increase, and  $N_t$  is the population size at time  $t$ . Because the method of tag recovery was very different between samples from Anticosti Island and those from Sable Island, pup production estimates from each recovery site were considered to be independent. Calculations were carried out on the nontransformed data and weighted by the inverse of their variance (Proc NLIN, SAS Institute Inc. 1988).

The dynamics of the population were reconstructed following the approach developed by Zwanenburg and Bowen (1990). A Leslie matrix type model (Leslie 1945) was developed incorporating information on age-specific reproductive rates (Hammill and Gosselin 1995) and estimates of survivorship which were modified to permit the population to grow at the observed rate of increase. Because this population was also subject to a government cull and a bounty hunt, removals from the population were incorporated into the population trajectory (Zwanenburg and Bowen 1990; Appendix). A stable age

**Table 1.** Estimates (*N*) of Gulf of St. Lawrence grey seal pup production during 1984–1986 and 1989–1990 based on the recovery of tags from animals shot in different years at Anticosti Island.

Year	Tags applied	Recaptures				<i>N</i>	SE	95% CI	Method
		1986	1987	1988	1992				
1984									
Early	928	5	2	4	0				
Late	481	10	1	3	0				
Eastern Shore	14	0	0	0	0				
Total captures		75	23	23	5	6955	1183	5 070 – 9 902	PPE
1985									
Early	1015	8	3	1	1				
Late	1103	12	3	4	0				
Eastern Shore	125	0	0	0	0				
Total captures		50	25	15	3	6391	877	4 940 – 8 470	PPE
1986									
Early	920	14	3	1	1				
Late	617	12	6	2	0				
Eastern Shore	144	2	1	0	0				
Total captures		87	29	13	9	5436	672	4 306 – 7 000	PPE
1989									
Early	1088				2				
Late	745				2				
Eastern Shore	172				0				
Total captures					21	8825	3164	4 694 – 19 651	PPE
1990									
Early	788				4				
Late	1431				3				
Total captures					32	9156	2652	5 444 – 17 180	PPE

distribution was generated iteratively for the population prior to 1967, when culling began. The model was initialized by adjusting pup production estimates for 1967 and allowing the model to run until we obtained the observed estimates of pup production for the 1984–1990 period.

## Results

### Anticosti Island mark–recapture experiment: 1984–1986 estimates

During the scientific collections undertaken at Anticosti Island in 1986, 1987, 1988, and 1992, the total number of animals shot (with the number of non-Sable tagged animals in parentheses) was 137 (36), 103 (42), 111 (57), 26 (9), and 39 (10) animals from the 1984, 1985, 1986, 1989, and 1990 cohorts, respectively (Table 1). Included in the total are 11, 10, 15, 5, and 3 animals that had been tagged on Sable Island during 1984, 1985, 1986, 1989, and 1990, respectively. Three tags were also recovered from Eastern Shore tagged seals in 1986. Tag loss was minimal; one tag was lost from each of the 1984 and 1985 shot samples from Anticosti Island. Since Sable Island tags accounted for <13% of the recoveries, animals that had lost tags were assumed to have come from the Gulf. Consequently, the number of animals tagged in the Gulf was increased by 1 (Table 1).

In the 1984–1986 data, the hypotheses of complete mixing and equal proportion of tags in the recovery samples were not rejected, but the number of captured animals was very small,

indicating that the chi-square test statistics had little value. Pup production for 1984, 1985, and 1986 using the PPE was estimated to be 6955 (SE = 1183; 95% CI = 5070–9902), 6391 (SE = 877; 95% CI = 4940–8470), and 5436 (SE = 672; 95% CI = 4306–7000) animals, respectively (Table 1).

Pup production in 1989 and 1990 was based on the recovery of tags collected from animals shot during August–September 1992. Four tags were recovered from the 1989 cohort: two from animals tagged early in the season and two animals tagged late in the season. Pup production was estimated to be 8825 (SE = 3164; 95% CI = 4694 – 19 651) excluding the animals killed in January 1989, before they had dispersed from the southern Gulf. If these animals are included, then the estimate increases to 10 437. Seven tags were recovered from the 1990 cohort: three from animals tagged early in the season and four from animals tagged late in the season. Pup production was estimated to be 9156 (SE = 2652; 95% CI = 5444 – 17 180) (Table 1).

### Sable Island mark–recapture experiment: 1984–1986 Gulf estimates

Beach surveys were conducted repeatedly during March–October 1984–1986 to obtain information on the number of Gulf tagged and untagged pups present on the island (Table 2). Compared with the Anticosti Island sample, tags from the Eastern Shore were more prevalent in samples obtained from Sable Island, representing 1% of the recoveries from 1984, 14% in 1985, and 13% of the Sable Island recoveries from 1986.

**Table 2.** Estimates (*N*) of Gulf of St. Lawrence grey seal pup production during 1984–1986 and 1989–1990 based on the recapture of pups on Sable Island during different months.

Year	Tags applied	Recapture No.					<i>N</i>	SE	95% CI	Method
		1	2	3	4	5				
<b>Pups</b>										
1984										
Early	928	0	2	5	7	1				
Late	481	1	2	2	3	0				
Eastern Shore	14	0	0	2	0	0				
Total captures		6	29	29	58	6	7431	1414	4 659 – 10 203	Darroch
1985										
Early	1015	0	16	8	1					
Late	1103	1	7	12	1					
Eastern Shore	125	0	4	3	0					
Total captures		66	169	137	15		— <sup>a</sup>			
1986										
Early	920	17	12	1						
Late	617	15	11	1						
Eastern Shore	144	4	7	0						
Total captures		183	153	11			8633	2827	3 093 – 14 174	Darroch
1989										
Early	1088	12	5							
Late	745	15	12							
Eastern Shore	172	1	3							
Total captures		102	73				7295	2118	3 143 – 11 446	Darroch
1990										
Early	788	16								
Late	1431	47								
Total captures		233					8116	846	6 661 – 10 028	PPE
<b>Yearlings</b>										
1985										
Early	1015	2								
Late	1103	5								
Eastern Shore	125	1								
Total captures		20					7767	1746	4 345 – 11 188	PPE

**Note:** Recapture Nos. 1–5 represent the number of tags in the different recapture samples (see text for details). The 1985 yearlings estimate is based on recoveries from animals shot in 1986.

<sup>a</sup> No estimate was obtained from the 1985 live-capture sample.

In 1984, the hypotheses for complete mixing was rejected ( $\chi^2 = 12.9$ ,  $df = 2$ ,  $p < 0.05$ ), but sample sizes were small (Table 2). Since tags applied along the Eastern Shore were also applied late in the season, pooling these recoveries with the late sample resulted in the complete mixing hypothesis no longer being rejected. Re-analysing the data resulted in an estimate of 7431 (SE = 1414; 95% CI = 4659 – 10 203), using the Darroch estimator.

In 1985, the hypotheses of complete mixing ( $\chi^2 = 6.7$ ,  $df = 2$ ) and equal proportion of marked animals in the recovery strata ( $\chi^2 = 10.1$ ,  $df = 3$ ) were both rejected ( $p < 0.05$ ), indicating that the PPE was not the appropriate model to use. In the recovery samples, tags from the Eastern Shore represented 13% of the recoveries, although they represented only 6% of the 2243 tags applied. Tags applied late in the season appeared to be underrepresented in May (recapture No. 2) sample but overrepresented in the June (recapture No. 3) recovery sample (Table 2). Tags applied along the Eastern Shore were also

applied late in the season. When these two strata were pooled, there were significant differences between the observed and expected number of recaptures, indicating that the model fit the data poorly ( $G^2 = 324$ ,  $df = 2$ ,  $p < 0.05$ ). We conclude that it is not possible to obtain an unbiased estimate from the 1985 live-recapture data.

During January–February 1986, a sample of yearlings was shot on Sable Island. In this sample the hypotheses of complete mixing and equal proportions were accepted and an estimate of 1985 pup production of 7767 (SE = 1746; 95% CI = 3196 – 12 259) animals using the Peterson method was obtained (Darroch method = 7727; SE = 2312; 95% CI = 3196 – 12 259) (Table 2).

In 1986, YOY were also resighted on Sable Island. In this sample the hypothesis for complete mixing was rejected ( $\chi^2 = 6.4$ ,  $df = 2$ ,  $p < 0.05$ ), indicating that the PPE was not appropriate. No estimate was obtained using the Darroch method. However, since tags along the Eastern Shore were

**Table 3.** Pup production estimates used to calculate rate of increase in Gulf of St. Lawrence grey seal pup production (Fig. 2) (SE in parentheses).

Year	Anticosti recaptures	Sable recaptures	Myers et al. 1997
1984	6 955 (1183)	7431 (1414)	
1985	6 391 (877)	7767 (1746)	
1986	5 436 (672)	8633 (2827)	
1989	10 437 (3164)	8907 (2118)	9 827 (1049)
1990	9 156 (2652)	8116 (846)	10 470 (1050)

also applied late in the year, the late and Eastern Shore recoveries were pooled. This resulted in an estimate of 8633 (SE = 2827; 95% CI = 3093 – 14 174) using the Darroch model (Table 2).

Grey seal pups were captured, examined for tags, and released on Sable Island during May–June 1989 and May 1990 (Table 2). In the May 1989 recapture sample, four animals had lost tags. We assumed that since Gulf animals account for only 17% of the total number of recaptures that the four animals missing tags had been born on Sable Island. This assumption is not unreasonable, as four double-tagged animals from the Gulf, captured in the May sample, had not lost any tags. In this sample, the hypothesis of complete mixing was rejected ( $\chi^2 = 8.0$ ,  $df = 2$ ,  $p < 0.05$ ). An analysis of the frequency of Gulf tags applied early and late in the season in the recaptures showed that there were a greater than expected number of tags applied late in the season in the June recapture sample ( $\chi^2 = 5.3$ ,  $df = 1$ ,  $p < 0.05$ ). Pup production using the Darroch method was 7307 (SE = 966; 95% CI = 5414–9199), but the model gave a poor fit to the data ( $G^2 = 61.7$ ,  $df = 1$ ,  $p < 0.05$ ). The hypothesis of complete mixing was still rejected when the late recoveries and the Eastern Shore were pooled ( $\chi^2 = 7.0$ ,  $df = 1$ ,  $p < 0.05$ ), but no significant differences were found between the expected and observed number of recaptures, indicating that the Darroch model was more appropriate. Pup production was estimated to be 7295 (SE = 2118; 95% CI = 3143 – 11 446) animals. Adding in the animals killed early in the spring results in an estimated pup production of 8907.

In 1990, 2219 tags were applied in the Gulf. No tags were applied on Île de Corp Mort in the southern Gulf or along the Eastern Shore. A total of 770 pups were captured, including 524 from Sable Island, 235 pups of Gulf origin (Table 2), and eight pups of unknown origin due to lost tags. Tags applied early in the season and tags applied late in the season were equally represented in the May 1990 Sable Island recapture sample. Total pup production was 8116 (SE = 846; 95% CI = 6661 – 10 027) (Table 2) assuming that all of the pups that had lost tags were of Sable Island origin.

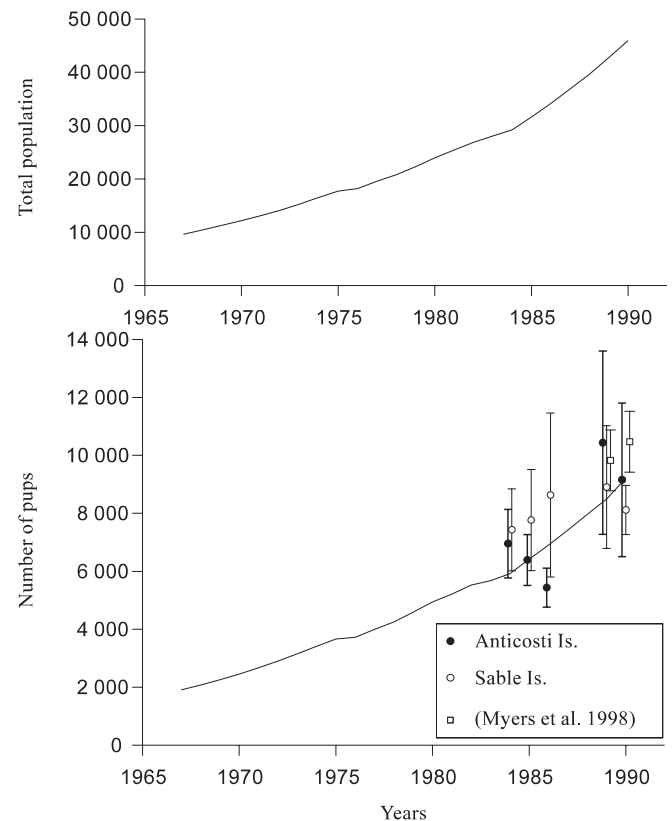
### Grey seal population growth rates

Two other estimates of pup production are available based on a within-season mark–recapture study completed by Myers et al. (1997). In this study, pup production in the Gulf was estimated to be 9827 (SE = 1049) in 1989 and 10 470 (SE = 1050) in 1990 (Table 3).

Using all data (Table 3), pup production is increasing at a rate of 7.4% (SE = 2.2) ( $N_0 = 5919$ ; SE = 572).

The change in population size was modelled from 1967

**Fig. 2.** Simulation of changes in pup production and total population size incorporating removals from the population (Zwanenburg and Bowen 1990; Appendix). The rate of population increase was determined using model parameters outlined in the text and estimates of pup production for 1984–1990.



through to 1990 using a rate of increase of 7.4%. Age-specific reproductive rates were set at 0.176, 0.861, and 0.875 for animals aged 4, 5, and >6 years, respectively (Hammill and Gosselin 1995). Using an adult survival rate of 0.96 (Zwanenburg and Bowen 1990), juvenile survival rate was estimated to be 0.522. During 1967–1990, pup production would have increased from 909 to 9216, while the total population increased from 9602 in 1967 to 45 936 in 1990 (Fig. 2) assuming that no changes occurred in the dynamics of the population over this period of time.

### Discussion

Mark–recapture techniques have been used successfully to census pinniped populations (Chapman and Johnson 1968; Bowen and Sergeant 1983). Logistically, they are relatively easy to complete, but difficulties are encountered in trying to satisfy model assumptions and in obtaining sufficient recaptures when using this approach on grey seals. We relied on samples from scientific collections and live captures on Sable Island for tag returns because there is currently no commercial hunt for grey seals, and returns from the bounty hunt are considered unreliable (Zwanenburg 1984). The Petersen estimator assumes a closed population, no tag loss, and equal catchability of marked and unmarked animals (Seber 1982) and the age of unmarked animals is determined without error. Most of our recoveries occurred over different sampling periods. When

this occurs, it is possible to pool the recovery data, whereby the estimator becomes the PPE, but two additional assumptions are required. These assumptions are that the recovery probabilities are constant across all strata and the expected ratio of marked to unmarked animals is constant across all recovery strata (Seber 1982).

The assumption of closure can be relaxed to some extent if emigration from the population or mortality applies equally to marked and unmarked animals. If there is immigration, then the Petersen method provides an estimate of the population at the time of the recapture sample. The assumption concerning tag loss can also be relaxed if some information is available to calculate this loss (Stobo and Horne 1994; Arnason et al. 1996). However, failure to satisfy the assumption of equal catchability results in biased estimates. Unfortunately, this bias can result in underestimates or overestimates, but the direction or magnitude of this bias cannot be determined from the available data. If the assumptions of closure and no tag loss are satisfied and if catchability varies between strata, but is constant within strata, then alternative methods such as the ML Darroch estimator may be used. Although these methods often produce a reasonable estimate that is less biased than the PPE, they are also often less precise (Arnason et al. 1996).

Errors in age determination may also affect the estimates if these errors result in a greater number or fewer individuals being included in the sample of unmarked animals. On Sable Island, no errors occurred in the live captures because only pups were captured at this site. Among older animals, there is a potential for age determination errors. However, the overall accuracy of age determination by reading grey seal canine tooth sections is around 93% and is 100% for animals between 3 and 6 years old (Mansfield 1991), which formed the majority of animals in the samples from Anticosti Island. Also the similarity among the estimates between samples indicates that errors in age determination of unmarked pups were not a significant factor.

Estimates of pup production obtained from the Sable Island data were higher than the Anticosti estimates in three of the five samples and generally had higher standard errors in spite of the greater number of animals in the recapture samples. We believe that the Sable Island estimates are more likely to be biased due to a combination of factors: the clumped distribution of tagged and untagged animals on the ice, the limited mobility of young pups, variability in ice drift patterns, and the short time between tag deployment and tag recovery. Also, the low number of Eastern Shore tags in the Anticosti samples and high proportion of these tags in the Sable Island recoveries compared with the total number of tags applied indicate that Eastern Shore animals are more likely to disperse to Sable Island than to the Gulf. If more animals were present along this shore than we could account for, then the greater tendency for Eastern Shore animals to disperse towards Sable Island would increase the number of untagged animals at this recovery site. In 1993, a new colony was discovered on Hay Island (G. Conway, Department of Fisheries and Oceans, Halifax, NS, personal communication) off the east coast of Cape Breton Island (Fig. 1). The following year, 1000 pups were tagged in this colony. Assuming a 7.4% rate of increase, there may have been as many as 477 pups born in this colony in 1984, or roughly two to four times the number of pups culled or tagged along this shore during 1984–1986. The dispersal of some of these

untagged pups towards Sable Island would inflate our estimate of pup production from the Sable Island recoveries. The Anticosti Island recoveries are less likely to be biased owing to the longer time period between tag deployment and tag recovery, which permits more mixing to occur. Unfortunately, the Anticosti data are difficult to test rigorously for significant levels of capture heterogeneity owing to the small number of recoveries.

Estimates of Gulf pup production for 1989–1990 were 7783–9681 animals including animals removed during the May hunt in 1989. These estimates are similar to estimates of 9827 (SE = 1049) to 10 470 (SE = 1050) obtained from a within-season mark–recapture experiment conducted in the southern Gulf during January and February 1989 and 1990 (Myers et al. 1998). These estimates do not include animals born along the Nova Scotia Eastern Shore and eastern United States. As outlined above, there are currently more animals found along the Eastern Shore than previously thought. Future surveys to assess grey seal pup production should include pups born in these non-core-area colonies, as their numbers are likely to continue to grow.

The Sable Island component of the Northwest Atlantic grey seal population is increasing at a rate of 12.6% per year (Stobo and Zwanenburg 1990). Assuming that there was little or no immigration, Zwanenburg and Bowen (1990) found that high survival rates of 0.96 and 0.787 for adults and juveniles, respectively, were required to achieve the 12.6% rate of increase. The Gulf component is increasing at a slower rate of 7.4% (SE = 2.2) per year. Assuming that no changes have occurred in the dynamics of this component of the population, then pup production has increased from 5925 animals in 1984 to 9329 in 1990, while the population has increased from 29 436 to 46 815 animals. These estimates of pup production underestimate the actual number of pups born because they do not take into account natural mortality prior to weaning. On Sable Island, Stobo and Zwanenburg (1990) estimated a natural mortality rate of 6–15% in the first month, which included both weaned and unweaned pups. During tagging operations on the ice the number of dead pups encountered is normally  $\leq 10\%$  (M.O. Hammill, unpublished data), but these observations do not take into account pups lost from the ice.

Pup production on Sable Island appears to be increasing at a higher rate than in the Gulf, although the significance of this is difficult to test because variability in factors such as adult survivorship was not included in our model. Since there is considerably overlap outside of the breeding season between the two groups (Stobo et al., 1990; Lavigne and Hammill 1993), adult survival rates should be the same. Reproductive rates are also similar for both (Hammill and Gosselin 1995). However, the Gulf component of the population has been hunted to a greater extent than the Sable Island component, and modelling changes in the Gulf population indicates that pup mortality rates are higher for this group, which consists largely of animals whelping on the unstable pack ice in the Gulf. Increased mortality could result from crushing by the ice, disruption of the mother–pup bond, or increased mortality after weaning owing to variability in ice drift and the availability of food. Emigration may be another factor. Pups expelled from the Gulf on the drifting ice may tend to remain on the Scotian Shelf, eventually moving to Sable Island to breed, or during years when there is little ice, pregnant females move to Sable Island and then return to this area in subsequent years if

reproduction had been successful. This emigration would also account for the lack of separation between Gulf and Sable Island grey seals based on analysis of mtDNA (Boskovic et al. 1996).

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## Appendix. Removals from the Gulf of St. Lawrence grey seal population from bounty and scientific collections.

Age (years)	1985	1986	1987	1988	1989	1990
0	113	180	593	90	1788	38
1	26	81	63	59	17	17
2	22	95	56	42	32	8
3	22	35	46	33	32	8
4	15	21	29	37	9	3
5	17	26	27	40	14	6
6	5	21	33	15	6	3
7	8	10	29	25	4	1
8	2	15	25	16	2	0
9	2	10	16	14	5	1
10	2	8	18	18	4	0
11	3	6	13	11	1	0
12	1	12	12	8	1	0
13	4	11	15	5	1	0
14	0	10	13	10	3	0
15	3	7	12	9	3	0
16	4	12	9	10	1	0
17	1	7	10	8	1	1
18	1	3	11	7	2	0
19	0	5	13	7	0	0
20	9	44	65	64	6	3