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USING MARK-RECAPTURE METHODS TO ESTIMATE PUP PRODUCTION OF HARP SEALS (*Phoca groenlandica*) IN THE GREENLAND SEA

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ABSTRACT

During the period 1968-1991 16,917 harp seal pups have been tagged in the Greenland Sea. From 1976 until 1991, there have been 468 recoveries. 73 of these, mostly drowned in fishing gear or part of Inuit catches at Greenland, are from areas outside the Greenland Sea, broadly covering the Norwegian coast, Iceland, East and West Greenland and Newfoundland. Recaptures made one year or more after tagging during the commercial catch operations in the Greenland Sea have been used to calculate pup production for several years during the period 1977-1991 by the Chapman mark-recapture estimator. These estimates, ranging from 40,000 to 115,000 but with no power to reveal any trend, show features that makes one suspecting that they might be seriously biased. The bias might be caused by violations of the randomness assumption and non-uniform distribution of tagged animals. A mechanism of non-permanent emigration is suggested to explain the source of the bias, but no data are available to correct it. A remedy that might be of limited value in management, would be to truncate the recapture data by using data collected from the fifth year onwards only, assuming that temporary emigrated seals have returned to the population upon reaching sexual maturity. Also inherent in the estimates is a bias of some + 5% caused by tag loss.

INTRODUCTION

The pack ice areas in the Greenland Sea between Jan Mayen and East Greenland (*'the West Ice'*) have been exploited by sealers for several decades. In the post-war period 1946-82 approximately 700,000 pups and 190,000 one year or older of harp seals (*Phoca groenlandica*) have been caught. Since 1982, when a ban on import of skins from seal pups was approved by the European Economic Community, the catches have been comparatively low and in the most recent years (1989-1992) directed towards moulting harp seals.

Despite this extensive catch history, little information is available on the sizes of the populations breeding in the Greenland Sea. However, during the last decade a number of recoveries of tagged harp seals in *West Ice* catches of known size and age composition suggests that this situation could be somewhat remedied. Tagging programs of harp and hooded seals have been conducted in the North Atlantic for several decades. The purpose of these taggings has primarily been to gain knowledge on migrations and distributions to resolve questions on population structure and stock identity. Known-age teeth from recaptured animals have also been used to study the formation of dentine and cementum layers to establish age reading procedures (Bowen, Sergeant and Øritsland 1983).

Since the late 1970-ies, Norwegian tagging efforts have been concentrated to the breeding lairs in the Greenland Sea area and then mainly to harp seals. In this paper we present and discuss mark-recapture estimates of annual pup production for most of the period 1977-1991 of harp seals breeding in the Greenland Sea.

MATERIALS AND METHODS

Tagging

Tagging has been conducted in breeding patches which are usually found within an area broadly delimited by the latitudes 70°N and 75°N and longitudes 20°W and 0°W. Through most of the years tagging has been carried out on an opportunistic basis as part of the research activities onboard commercial vessels during their catch operations. This has restricted the possibilities of distributing tagging effort throughout the breeding season and area. In the years 1983-1988 Governmental subsidies, partly allocated to facilitate research, made it easier to tag a larger number of pups. During the years 1989-1991 tagging was carried out from research vessels, mainly by using helicopter to distribute personell.

Harp seal pups have been tagged with individually numbered Dalton Rototags, usually in the left hind flippers. Pups have been tagged as available in the breeding lairs, regardless of stages (whitecoat, bedlamers etc.). Since taggings have been partly carried out concurrently with sealing operations, tagged pups have been marked with paint to avoid immediate recaptures (Rasmussen and Øritsland 1964). This has also been a useful approach during helicopter marking, thus avoiding to spend effort in previously visited areas.

Recoveries

The name and adress of the Institute of Marine Research are imprinted on the Rototags, and a reward is paid for return information on date and position of recapture. Recaptures are mainly reported from commercial sealing, incidental catches in fishery and inuit catches at Greenland. Commercial sealing in the Greenland Sea has been directed towards harp and hooded seals. Both species form whelping patches there from mid-March to the beginning of April, and towards the end of April, one year or older harp seals form moulting lairs. The sealers are well aware of the marking program and many of them have participated in the tagging efforts.

Pup production estimates

Catching pups was allowed in the years up to and including 1988, which inevitably implied that some tagged pups were caught already within the same season. These data are, however, useless for mark-recapture estimates because they clearly violate the randomness assumptions of sampling. The pup production estimates presented here are based upon recaptures one year or more after the year of tagging. We have used the Chapman modification of the Petersen estimator (Seber 1982) to estimate the number of pups N_i borne in year **i** as

$$N_i = [\,(M_i+1)(C+1)\ /\ (R+1)\,] - 1 + PC_i \quad \text{(eq. 1)}$$

where M_i is the number of pups *effectively marked* at the end of the breeding season in year **i** (i.e. the number of pups really tagged minus the number of within season recoveries), and **R** is the number of tags recovered in the accumulated Greenland Sea commercial catches C of one year or older seals from that cohort the following **j** seasons. Thus $R= \Sigma_{j=1,n}R_{i+j}$ and $C= \Sigma_{j=1,n}C_{i+j}$ when the second sample has been taken over the next **n** years after tagging. Accumulated data have been used to increase sample sizes as these are small for other than the most recent cohorts. $\mathbf{PC}_i$ is a correction term for the pup catch in year **i**, added to account for removals prior to the experiment.

Following Seber (1982), several assumptions must hold for N_i to be a valid estimator:

1) The population is closed (i.e. N constant).
2) The second sample is a simple random sample.
3) Animals do not loose their marks in the time between marking and recapture.
4) All marks are reported on recovery in the second sample.

The variance of N_i has been calculated as suggested in Seber (1982) as

$$var(N_i) = [(M_i+1)(C+1)(M_i-R)(C-R)] / [(R+1)^2(R+2)] \quad \text{(eq. 2)},$$

and approximate 95% confidence limits as

$$N_i \pm 1.96 \, sqrt\,[var(N_i)].$$

The number of seals in the second sample over **n** following years has been calculated as the occurence of the year **i** cohort in the total catches in the Greenland Sea as revealed in age samples from Norwegian catches.

Age samples

Over the period relevant to the pup production estimates (1978-92), age samples have usually been collected annually onboard one or two commercially operating Norwegian vessels. The absolute sample sizes have varied as have the catches, but usually the age samples have comprised from 25% to more than 90% of the Norwegian catches of one year and older seals. These age samples have been used for the total catches, i.e. the Norwegian plus the Soviet catches in the Greenland Sea, where appropriate. In 1985 and 1986 only a few adult seals were taken (31 and 256 respectively), and for these the age distribution in the 1986 Soviet scientific catch of 250 females has been used.

We also realize that the estimates presented in this paper could be refined by using age samples where available for Soviet catches. While the Norwegian vessels usually have operated within the same period of time and area, the Soviet catches have often been taken later in the season. Unpublished data indicate that there might be a considerable segregation both with regard to sex and age during the moulting season. However, since the Soviet catches account for approximately 12.5% only of the total catches of interest, we do not expect that the approach taken would cause a major effect on our conclusions.

Age readings have usually been assigned exact values, but often (range 1%-18% of total in recent age samples) a reader may only be able to determine a minimum age for a tooth section, meaning that one or more additional annuli probably are present. Such problems seem to arise at approximately ten annuli and above. We have used all age readings in calculating age proportions, interpreting the above mentioned sections as minimum age readings. This might introduce a slight overestimation in the 1977 and 1978 pup production estimates.

Evaluations (not presented here) of age determinations based on dental annuli indicate that they might be subject both to measurement and systematic errors. We have not tried to account for such errors in the calculations presented here, but note that measurement errors would add to the uncertainty in the pup production estimates, while it is not at all clear in which direction estimates would be biased if there are systematic errors of the kind mentioned above.

RESULTS AND DISCUSSION

Pup production estimates

Pup production estimates based on recoveries accumulated over the years up to and including 1991 are summarized in Table 1. The coefficients of variation for these estimates are typically less than 0.15 (range 0.10-0.27). Although the estimates span a wide range, they can hardly be told apart by their 95% confidence limits with the possible exception of the highest ones. Basic data are given in Tables 2 and 3; preliminary data from the 1992 season are included in all calculations with the exception of those in Table 1. The standard estimates given in Table 4 together with their associated 95% confidence limits are shown in Fig 1. In Fig 2 the cohort estimates are plotted as a function of years with accumulated data. There are two apparent features of the estimates that are unsatisfactory and need to be discussed:

(1) The point estimates tend to either increase or decrease for a specific cohort as years pass (as illustrated in Fig 2), while the ratio trend of marked to unmarked animals within a cohort should be constant if the underlying assumptions do hold;

(2) The pup production estimates seem to fall into two broad categories (Fig 1); one with estimates around 40-55,000 (seven cohort estimates) and one with estimates two to three times of that - 100-115,000 (three cohort estimates).

At this stage we feel quite confident that the potential problems mentioned above with regard to the age proportions that determine the catch component C in equation 1 are of minor concern. We note that none of the estimates given in Table 1 are based on lesser than 10 recoveries, implying that bias in equation 1 due to small sample sizes should be negligible (Seber 1982). In the following we therefore concentrate on the assumptions underlying equation 1.

Population closed

Since natural mortality and catches remove animals from the cohort, it is not closed. Since there is no reason to believe that losses operate differentially on marked and unmarked individuals, N_t by equation 1 is still a valid estimate. It might be hypothesised that emigration and immigration take place and thereby confound the estimates. Non-permanent emigration will be postponed until further for a separate discussion item, and permanent emigration would be equivalent to mortality. Immigration would give a positive bias in the mark-recapture estimates. Moreover, the increasing trends (Figure 2) could be explained as continuos additions from other sources, while the decreasing trends would result when early immigrants disappeared. These explanations seem to be contradictory as a general clue to the observed patterns, but might have some merit in special cases. Although a transatlantic migration of a one year old harp seal tagged in the Gulf of St. Lawrence and recaptured northwest of Andenes, northern Norway (Sergeant 1973), has been reported, there have been no recaptures in the *West Ice* of harp seals tagged at Newfoundland or in the White Sea. An extensive marking programme has been going on at Newfoundland for several decades, and there was a considerable tagging effort in the White Sea in the 60-ies (Popov 1970) followed up by recent taggings (1629 pups in 1989 and 3646 pups in 1990). We consider it rather improbable that no recoveries from Newfoundland have shown up in *West Ice* catches if immigrations from that area is significant. On the other hand, since a negligible number of pups has been tagged in the White Sea during the period 1969-1988, one could argue that the cohorts with high pup production estimates (1984/85/89) were influenced by immigrants from the White Sea population. That stock was rapidly increasing around 1980 (ICES 1990). Depleted resources in the Barents Sea might have enforced a surplus pup production to leave the usual living grounds to survive, until a drastic reduction in the number of breeding females has adapted the population to the prevailing conditions. The large seal invasions to the Norwegian coastlines in 1986-88 might have been a transitional phase where these previous emigrants searched for their imminent breeding/moulting grounds. The above speculations are not testable for the 1984 and 1985 cohorts, while the situation for the 1989 cohort might be illuminated in the following way: In 1989 1,629 harp seal pups were tagged in the White Sea; that is approximately one tagged pup in 40, assuming the 1988 aerial estimate of 71,000 breeding females (ICES 1990) as a proxy for pup production. In 1990 and 1991 the estimated total catch from the 1989 cohort in the *West Ice* was 1,923 animals, with 51 recoveries - all tagged in the *West Ice* - which is also around one tagged in 40 individuals. Let us say that 50,000 pups were borne in the *West Ice* in 1989. Then the 51 recoveries should be accounted for by less than 700 animals of the total catch, given that 3796 pups were tagged in 1989. We would then expect around 30 recoveries from the White Sea in these catches, which is certainly not in accordance with the zero observation.

Tag loss

Tag loss in itself is of great concern in mark-recapture experiments as it introduces positive bias in population estimates. Therefore it is often customary to use only the next year's recapture information for such data, assuming that tag loss is an increasing problem with time. In the present case there are grave objections to that procedure, as will be elaborated upon later.

It might be suggested that tag loss could explain why we observe an increasing trend in most of the cohort estimates as data accumulate over the years. Unfortunately, double tagging experiments have not been carried out routinely to check the tag loss assumption. Bowen and Sergeant (1983) found that loss of Rototags in harp seals occurs shortly after the tags are applied and subsequent losses are negligible, at least until the tags become worn or brittle. If the tags are lost only during the first year after application and at a probability of 0.25, all the serial estimates of, say, the 1978 cohort are positively biased, although this should not induce a trend in the series. The bias in the final 1978 estimate would then be +21%. To get an idea of how large the bias in the pup production estimates caused by tag loss might be, Table 1 has been provided with the approximate biases that would arise from loss probabilities π (unspecified time interval, although thought to take place shortly after tagging) of 0.25 (see above), 0.15 and 0.05. The justification for the probability of 0.05 is found in Bowen and Sergeant (1983), who conducted a double-tagging experiment for Rototags on harp seals living under similar conditions in the Northwest Atlantic. They estimated a tag loss rate of 0.051 ± 0.0081 (SE) from data pooled over the first three months after tag application, with no evidence of increasing tag loss with time. We consider their findings to be highly appropriate and applicable also to our results. So if tag loss is to account for increasing serial trends in estimates, there has to be further tag losses as years pass. We therefore tend to conclude that the serial trends in the cohort estimates as shown in Fig 2 must be caused by other factors than tag losses only.

Non-reporting of recoveries

A topic closely related to tag loss is non-reporting of recoveries. During the period covered by this study, only a few vessels have participated in the catching operations. Institute personell have often been onboard these vessels, and the crew members have been well aware of the tagging programme. If not detected at an earlier stage, the tag is usually recognized when the seals are skinned. However, tags might occasionally be overlooked. During the catching season in 1989 we received reports on two occasions and in 1990 on one occasion that the remains of a processed seal had been thrown overboard when it was recognized that it had a tag, however too late to identify it. We therefore have to realize that some unknown positive bias is introduced to the estimates from such losses.

Violations of sampling assumptions and non-permanent emigration

Segregational behaviour and non-random mixing would be detrimental to mark-recapture estimates. One might become critical when one is learning that a vessel in a consecutive two-day catch of 822 animals, recaptured four two year olds (two females and two males) which were all tagged on the same date, and four six year olds (also two females and two males, but none of them tagged on the same date). We must, however, bear in mind that each year only a few dates are available for marking. On an average, the pooled recapture rates are similar for the different vessels operating within the same year. Thus there are no apparent violations of the randomness assumptions. A further breakdown of the data by cohorts and daily catch rates proved to be impossible due to obvious errors in the data sets and small sample sizes.

While we have pointed out that the discussions so far have failed to explain the observed results entirely satisfactorily, a mechanism that could possibly explain both serial trends (positive and negative) as well as large variations in estimates might be suggested. The basis for these speculations is that recoveries of harp seals tagged in the Greenland Sea have been reported from a vast area extending from Newfoundland to the Barents Sea, most of them young immature animals. Tagged animals from some of the cohorts (for example 1984) seem to have been more prone to go to other areas, depending on ice and prevailing weather conditions, as discussed earlier. For simplicity, in our model we will assume that the pup production P_{true} in any year can be divided into two components, one "normal" component P_1 and one "emigrating" component P_2. P_1 is supposed to follow a normal migration cycle, whatever that might be, but at any rate returning to the *West Ice* next year for moulting.

We suggest that P_2 at least temporarily (> one year) leaves the normal cycle, and its members are therefore not available for the next year's moulting season. The assignment of a pup to either of these components takes place at birth, for example determined by location in a breeding patch, where those at the outskirts might be more prone to be taken away by prevailing weather and ice conditions. Let us say that $P_1 = \alpha P_{true}$ and $P_2 = (1-\alpha)P_{true}$. If we then place **M** tags among these pups, a fraction βM in component P_1 and $(1-\beta)M$ in component P_2, our estimate of pup production (by the simple Petersen estimator) based on the next year's recaptures will be $P_{est1} = (\alpha/\beta)P_{true}$ ($\alpha>0$, $\beta>0$). That is, proportional tagging ($\alpha = \beta$) is the only way of achieving an unbiased estimate.

For illustration, let a proportion γP_2 return to the normal moulting grounds the second year. Then the estimate of pup production based on that year's data will be $P_{est1} = [(\alpha+\gamma(1-\alpha))/(\beta+\gamma(1-\beta))]P_{true}$. Once again, $\alpha = \beta$ is a prerequisite for this to be an unbiased estimate, if not $\gamma = 1$. If the estimate is biased ($\alpha \neq \beta$), the return rate γ will determine how fast the estimates approach the true value over years. This motivated the following procedures for alternative estimations of pup production: 1) Given that the first year after tagging generally is the more sensitive one to the assumptions of uniform mixing, estimates were calculated according to equation 1, but with **j = 2**; 2) By the assumption that all emigrants would have returned to the population when sexually mature, equation 1 was calculated with **j = 5**. The results are given in Table 4. It must also be said that the within cohort serial trends did not change significantly with procedure 1 as compared to the standard procedure (procedure 2 reveals too few points), which might indicate that the proposed return rate γ is rather small the first year. The estimates in Table 4 might however indicate that the thoughts advanced above deserve some attention. We would also point out that for the years 1984 and 1985, when tagging was conducted from catching vessels which were unable to locate the main breeding patches for harp seals (pup catch approximately zero), the estimates are probably positively biased ($\alpha > \beta$). It is not understood why the estimates from 1990 and 1991 are so different from that for 1989, since tagging was conducted from research vessels thought to be in the main whelping grounds all these years.

CONCLUSIONS

Pup production estimates calculated from accumulated data from the first year after tagging onwards, show a variable pattern which might be accounted for by assuming that non-permanent emigrations really take place. Estimates will then depend on 1) how large the fraction $(1-\alpha)$ is that leaves the normal cycle, 2) the fraction $(1-\beta)$ of tags placed in that leaving portion, and 3) the fraction γ that returns to the normal cycle after two or more years. We think that the trends observed over years within the cohorts indicate that many non-permanently emigrated seals do not return until they are sexually mature, and thus the best estimator of pup production would be equation 1 left-truncated so that **j=5**.

Since the preferred estimator requires a rather long time-lag, it is not especially useful for management purposes that need a continuous surveillance. That is, for short-term decisions we seem to be left with estimates based upon the first few years after tagging. These estimates might be biased in either direction, depending upon the earlier discussed parameters α and β. The only way that these estimates can be unbiased, is that pups have been tagged proportionally in a consistent manner. It is difficult to imagine how that could be done without a simultaneously dedicated survey.

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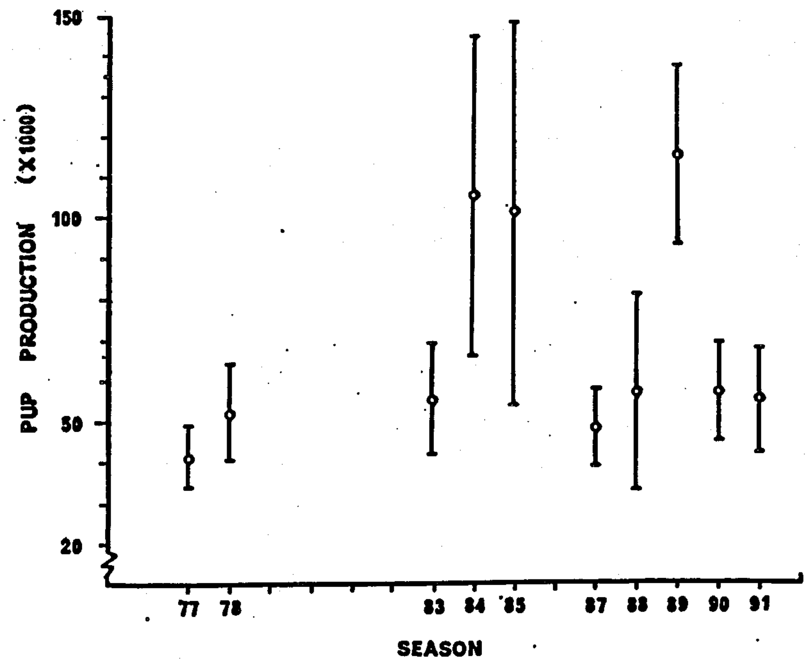

Figure 1. Pup production estimates by year based on accumulated data up to and including 1992. The bars illustrate the 95% confidence regions around the point estimates.

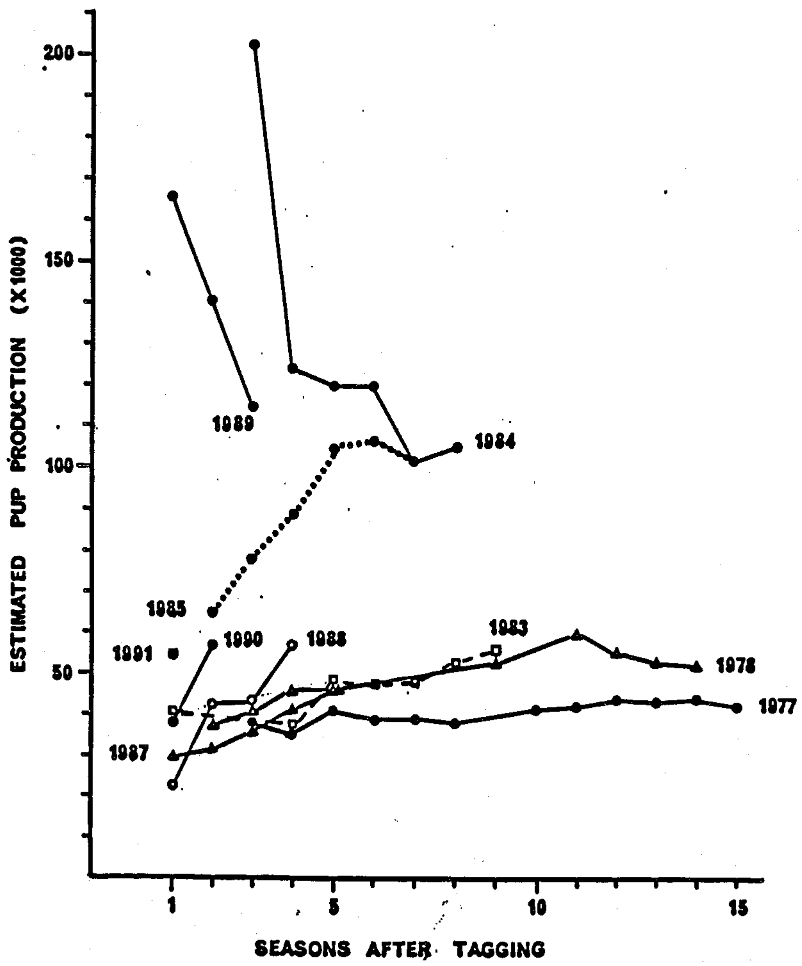

Figure 2. Cohort pup production estimates plotted as a function of years with accumulated data.

Table 1. Pup production in selected years as calculated from accumulated data up to and including 1991. In addition to the estimate are given coefficients of variation, lower and upper 95% confidence limits, biases in estimates for tag loss probabilities of 0.25, 0.15 and 0.05, and trends within cohorts as data accumulate (P is the probability of the t-test for the trend).

	PUP PRODUCTION				TAG LOSS BIAS (%)			TREND	
YEAR	Estimate	c.v.	Lower	Upper	0.25	0.15	0.05	%	P
1977	43,883	0.10	35,348	52,418	19	11	3	0.8	0.18
1978	54,514	0.12	41,140	67,888	21	12	4	3.5	0.00
1983	51,779	0.13	38,378	65,179	29	16	5	4.1	0.01
1984	105,735	0.21	62,260	149,210	33	18	5	-13.7	0.10
1985	106,784	0.27	49,759	163,809	33	18	5	13.1	0.00
1987	40,987	0.11	32,318	49,656	25	14	4	11.4	0.01
1988	42,966	0.21	25,558	60,374	22	12	4	32.0	0.30
1989	140,501	0.13	103,455	177,547	33	18	5	-15.3	.
1990	38,801	0.14	27,875	49,727	33	18	5	.	.

Table 2. number of recaptures by year for each cohort and accumulated recaptures and catches used in the calculations.

	YEAR OF RECAPTURE WITHIN THE GREENLAND SEA															CUMULAITVE	
YEAR	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	R	CATCH
1977	0	1	6	5	1	3	2	1	0	6	3	3	4	2	5	42	2371
1978		0	7	2	1	1	0	0	0	5	0	3	5	3	2	29	2279
1983							8	0	0	10	7	6	5	6	6	48	1897
1984								0	0	2	7	3	3	5	4	24	2056
1985									0	4	4	1	1	1	4	15	2618
1987											30	10	7	2	14	63	1252
1988												7	1	2	1	11	1714
1989													31	20	45	96	2945
1990														42	34	76	1452
1991															65	65	1090

Table 3. Number of effective taggings M and pup catches PC used for the calculation of pup production.

YEAR, i	EFFECTIVELY TAGGED	PUP CATCH
1977	480	15305
1978	488	16424
1983	1301	5005
1984	1328	199
1985	612	535
1987	2073	7961
1988	316	11493
1989	3796	37
1990	3004	26
1991	3327	0

Table 4. Alternative pup production estimates based on a variety of assumptions; tag loss as a problem increasing with time (next year's recaptures only), and returns of non-permanently emigrated seals (see text) after j=2 and j=5 years. For some years "next year's recaptures" mean the first year after tagging (given in parentheses) with recapture information. "Standard estimates" refer to those derived from all accumulated data up to and including 1992.

YEAR	STANDARD ESTIMATES	NEXT YEAR RECAPTURES	j = 2	j = 5
1977	41,839	45,715 (+2)	41,605	43,809
1978	52,388	37,800 (+2)	50,903	54,056
1983	55,434	40,407	57,534	64,907
1984	105,346	202,568 (+3)	105,346	88,100
1985	100,885	65,272 (+2)	100,885	103,018
1987	48,561	29,953	64,394	71,240
1988	56,795	23,105	101,703	-
1989	115,353	165,806	89,202	-
1990	56,720	38,801	77,200	-
1991	54,987	54,987	-	-