

Not to be cited without
permission of the authors¹

Canadian Atlantic Fisheries
Scientific Advisory Committee

CAFSAC Research Document 84/9

Ne pas citer sans
autorisation des auteurs¹

Comité scientifique consultatif des
pêches canadiennes dans l'Atlantique

CSCPCA Document de recherche 84/9

**An Assessment of the Northwest Atlantic
Grey Seal (Halichoerus grypus) Population for 1983**

by

K. Zwanenburg

Marine Fish Division
Bedford Institute of Oceanography
P.O. Box 1006, Dartmouth
Nova Scotia B2Y 4A2

¹This series documents the scientific basis for fisheries management advice in Atlantic Canada. As such, it addresses the issues of the day in the time frames required and the Research Documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Research Documents are produced in the official language in which they are provided to the Secretariat by the author.

¹Cette série documente les bases scientifiques des conseils de gestion des pêches sur la côte atlantique du Canada. Comme telle, elle couvre les problèmes actuels selon les échéanciers voulus et les Documents de recherche qu'elle contient ne doivent pas être considérés comme des énoncés finals sur les sujets traités mais plutôt comme des rapports d'étape sur des études en cours.

Les Documents de recherche sont publiés dans la langue officielle utilisée par les auteurs dans le manuscrit envoyé du secrétariat.

Abstract

This document outlines an assessment of the Northwest Atlantic grey seal (Halichoerus grypus) population. The primary data source was a long-term, large-scale mark and recapture experiment which was initiated in 1977. Each year since 1977 all pups whelped on Sable Island (Nova Scotia) have been marked. Returns of these marks, via a bounty system, have allowed for estimates of total population pup production since 1977. This bounty system has also provided data on population age structure, age specific mortality rates, and reproductive rates. Knowledge of population pup production coupled with data on age specific fecundity and mortality schedules allowed for definition of a Leslie type transition matrix which was in turn used to predict both age specific and total population sizes. Using these methods the 1+ population size in 1983 was estimated at between 71,000 and 125,000 animals. These wide confidence intervals are evidence of the uncertainties inherent in these calculations.

Résumé

Ce document donne un aperçu de l'évaluation de la population de phoques gris (Halichoerus grypus) dans le nord-est de l'Atlantique. La principale source de données est l'expérience de marquage et de recapture à long terme, entreprise en 1977. Chaque année depuis 1977, tous les chiots de l'île de Sable en Nouvelle-Ecosse ont été marqués. La récupération de ces marques grâce à l'attribution de primes aux chasseurs, a permis d'évaluer la population totale des chiots depuis 1977. L'attribution de primes a également permis de réunir des données sur la structure d'âge de la population, le taux de mortalité par âge et le taux de reproduction. Les données sur la reproduction, jointes à celles sur la fécondité et la mortalité par âge ont donné lieu à une matrice de transition semblable à celle de Leslie. Cette matrice a permis de faire des prévisions quant à la taille de la population globale et de la population par âge. Ainsi, la taille de la population d'âge 1+ en 1983 devrait varier de 71 000 à 125 000 phoques. Ce large intervalle de confiance illustre bien les incertitudes inhérentes à ce genre de calculs.

The Data Sources

Several sources of data are available from which the status of Northwest Atlantic grey seal population was assessed. In 1968, 1969, 1970, 1975, and 1982 random samples of grey seals were shot by trained collectors. Each animal was aged by counting annuli in the cementum of the canine teeth (Laws 1953, Hewer 1964). The age distribution of these samples are given in Table 1. From 1967 to the present the Department of Fisheries and Oceans has carried out an annual kill of grey seals in the Gulf of St. Lawrence and on the Islands off the eastern shore of Nova Scotia. These animals, which include both pups and adults, are sexed but not aged. The numbers killed during each year's operation are not counted but estimated (Table 2). From 1976 to the present, in the Maritimes and Quebec, a bounty has been paid for the return of grey seal lower jaws. These jaws provide another source of aged data (Table 3).

In addition to information on the age structure of the population a large tagging experiment has been carried out since 1977.

The Tagging Experiment

Since 1977 we have tagged 95-100% of all pups born on Sable Island. A unique colour of tag has been used for each year of the program to simplify categorizing subsequent recaptures. All tags are applied through the webbing of one or other hind flipper. A summary of the numbers of tags applied in each year of the experiment is given below.

Year	1977	1978	1979	1980	1981	1982	1983
No. Tagged	1967	2266	2720	3250	2843	4138	4702
(Gulf)	-	-	460	160	-	652	72
Total	1967	2266	3180	3410	2843	4790	4774

The Mark Recapture Model Employed

In the previous assessment of the Northwest Atlantic grey seal population (Zwanenburg *et al.* 1981) a simple Petersen mark-recapture model was used to estimate pup production. This model does not allow more than a single recapture interval to contribute to the final estimates. It was felt that this was an inefficient use of available data in that for most marked cohorts a number of years of data are available. The mark recapture model developed by Paloheimo (1963) and later described by Seber (1982) allows for the results of a number of consecutive recapture intervals to contribute to the estimate. The notation employed is due to Seber (1982). Let:

N_0 = the initial size of the total population
 M_0 = the initial size of the marked population

n_i = the size of the i th sample removed from the population
 m_i = the number of marked individuals in the i th sample

$$y_i = m_i/n_i$$

Then if the assumptions of the Petersen method hold for each sample;

$$\hat{N}_0 = M_0 \sum n_i / \sum m_i,$$

or, adjusting for bias,

$$\hat{N}_0 = M_0 (\sum n_i + 1) / (\sum m_i + 1)$$

which is simply a Petersen estimate based on data pooled for all recapture intervals. A major assumption of this model is the constancy of m_i/n_i over all catch intervals. This was checked by plotting y_i vs i for the recaptures from each cohort and looking for anomalies. The validity of the assumptions underlying the Petersen model itself are discussed below.

I. Equal Natural Mortality of Marked and Unmarked Individuals

Several years worth of observations made during the tagging operations on Sable Island indicate that tagging results in little or no physical damage to the pups. Longer term observation extending over several weeks or months gives no evidence of increased morbidity or mortality as a result of tag application. We have made some recent observations indicating that tagging of newborn pups (yellow jackets) may result in premature abandonment by the female. This abandonment is most evident if the female and her pup are disturbed within the first several hours post-partum. During this time the mother-pup bond is not yet firmly established (Fogden 1971, Burton et al. 1975) and can be easily broken. For this reason we avoid attempting to tag these newborn animals thereby reducing the probability of abandonment and subsequent mortality. After several days, and up to several weeks post-partum the pup can be temporarily removed from the female, tagged, and returned without any indication that abandonment will result. Suckling usually lasts between 17 and 19 days (Fogden 1968, Boness and James (1979), if a mother and pup are disturbed around this time she is again more likely to abandon her pup; however, after this long period of suckling the pup does not appear to suffer any ill effects as a result of abandonment.

To aid in the identification of animals already tagged a small (3 x 10 cm) strip of brightly coloured plasticized ribbon is attached to each tag. This strip of plastic also facilitates finding the tags on animals which are shot for the bounty later in the year. It has been suggested that this small marker could be leading to increased mortality as a result of increased predation. As judged by the prevalence of shark bite scars on the adult seals we have observed (approximately 10% of the adults on Sable Island bear some shark bite scars) we may tentatively conclude that sharks are an important predator of grey seals. Pups bearing scars have not been observed (although pieces of pup carcasses bearing tooth marks have been

found) and it is likely that these encounters are usually fatal. Since sharks hunt mostly by sense of smell and through use of the pressure sensitive lateral line system it is unlikely that a small brightly coloured tag attached to a hind flipper would increase the pups' probability of detection by sharks. However, this assumption has not yet been verified. There is also some indication that the tag applied to the hind flipper may cause mortality by entangling the animal in inshore gillnets. The fact that tags have been found caught in the nets while the seal has subsequently escaped, indicates that tags may increase the seals probability of becoming entangled; however, the number of times this leads to drowning rather than tag loss cannot be determined from the available data. It therefore appears that there is no firm evidence to suggest that tagged animals suffer a higher rate of natural mortality than untagged animals.

II. Equal Vulnerability to Hunting

The second assumption of the Petersen mark recapture model states that marked animals must be as vulnerable to hunting as unmarked animals. This assumption is testable by examining the constancy of y_i (m_i/n_i) for successive recapture intervals as stated in the description of the model. The behaviour of y_i is shown in Figure 1. From this we conclude that there is no trend in values of y_i over time indicating that marked and unmarked animals remain at a stable proportion over time.

III. Tag Loss

The third assumption of the Petersen model is that marked animals do not lose their marks. Estimates of tag loss in grey seals to date are based on minimal data and require further study to adequately quantify. Tag loss is presently assumed to follow the pattern observed in harp seals which indicates that a certain proportion of tags are lost soon after application and that subsequent tag loss is negligible. Bowen (1983) found a loss rate of 5% for ice breeding harps, at present it is assumed that the land breeding greys suffer a loss rate of 0.10. Estimates of N_0 were corrected by reducing the marked population (M_0) by 10%.

IV. Random Mixing of Marks

The fourth assumption states that marked animals become randomly mixed with unmarked animals or that the distribution of hunting effort is proportional to the number of animals present in different parts of the animals' distribution. The fact that a relatively large proportion of the total number of pup tags turned in each year come from Newfoundland suggests that a substantial number of pups reside there. The lack of untagged returns is due to the absence of bounty payments in Newfoundland. We are then faced with an area of the grey seals' distribution which contains a relatively large proportion of the total populations but where distribution of marked to unmarked animals or hunting pressure cannot be determined.

If the remainder of the grey seals' distribution is examined; we may test the validity of the assumption of random distribution of marks by

looking at the pattern of the ratio of tagged to untagged returns. If these exhibit a uniform value throughout the area of distribution we may assume that random mixing has occurred. Tagged to untagged ratio of returns are plotted by 10' squares on Figure 2. It is evident that their distribution is far from uniform. Along the Southwest coast of Nova Scotia this ratio ranges in value from 1.5 to 9.0 indicating that tagged pups are 1.5 to 9.0 times as abundant as untagged pups. This may be due to the inshore migration of a relatively large number of tagged pups off Sable Island. It may also indicate that relatively few untagged, Gulf born pups, venture into these areas where they would dilute these numbers. The outward migration of Gulf born pups is evidenced by the decreasing ratio around the shores of Cape Breton, here values range from 0.25 - 2.0. In the Southern Gulf of St. Lawrence, specifically in the Northumberland Strait, and in the environs of the Magdalen Islands the ratio ranges from 0.10 to 0.60 indicating a preponderance of untagged Gulf born animals. Along the Northern shore of the Gulf the ratio of tagged to untagged animals ranges from 0.13 to 5.0. The highest value seems highly unlikely in view of the values in adjacent squares. It may be that this anomaly is the result of a chance selection of tags as opposed to jaws in this particular area. It thus appears that the distribution of marks, at least among grey seal pups, is not random. For these reasons returns at age 0+ were not included in estimates of \hat{N}_0 .

If we examine these same ratios for age 1+ animals (Figure 3) we observe that their distribution is much more uniform although a vestige of the pattern observed in the pups remains. These data are somewhat more difficult to interpret because of the smaller number of returns and the resulting sparsity of calculable ratios. If the size of the grid units is increased to 30' squares the patterns are somewhat easier to discern (Figure 3). Again we observe that tagged animals appear to be somewhat over represented on the Southwest coast of Nova Scotia although this feature is not as prominent as was the case for pups.

The reduced patterning of returns at age 1+ seems to imply that marks become more uniformly distributed in the population at large as they grow older. If this is the case the use of the present recapture model should improve estimates of \hat{N}_0 since it uses pooled data for several recapture intervals. It would be desirable if the actual patterns observed could be incorporated into a mark recapture model, however, no satisfactory method of achieving this has yet been identified.

V. Recognition and Reporting of Marks

The next explicit assumption of the Petersen mark recapture method states that all marks must be recognized and reported on recovery. Earlier in the text it was stated that for the past several years brightly coloured plastic flags were attached to the tags. This makes it very easy to determine whether or not an animal has been tagged. The second half of this assumption which states that all marks must be reported when recognized is rather more difficult to evaluate.

The marked and unmarked animals which come into nearshore areas other than Newfoundland become available to recapture. The individuals from whom returns are received can be grouped into three major categories: those who actively hunt the seals in order to collect the bounty reward, those who actively hunt the seals to protect a fishing installation or fishing ground with the bounty reward as a secondary consideration, or recaptures of an accidental nature. Each of these classes of recaptures presents its own unique set of limitations or problems in terms of using the data to estimate pup abundance in the mark recapture model presently employed. Returns from these three groups can be classed under the following headings for purposes of discussion.

Tags Only Returns

These returns appear to be biased toward tagged animals. Since no jaw accompanied the tag, the collector is either not aware of the bounty paid for its return or not prepared to remove the jaw. In either case this individual is likely to select only tags for return and ignore untagged animals. This will inflate the ratio of tagged to untagged animals and alter estimates of abundance.

Tag and Jaw Returns

These returns can be broken down into two groups. The first are those received from known bounty hunters, individuals who are known to actively pursue grey seals for the purposes of collecting the bounty reward. These individuals are well aware of the fact that a bonus will be paid for tags. We feel that this group of returns is most likely to represent the actual proportions of marked and unmarked animals found in the accessible populations. The second group of jaw and tag returns are those received from persons other than bounty hunters. These returns may again be biased for tagged animals for reasons similar to those noted for tag only returns. A non-bounty hunter who finds a dead tagged seal and who is aware of the bounty paid, may submit both the tag and the jaw. However, since hunting the seals for bounty is not a directed effort in this case it is quite likely that any untagged animals will not be reported. Therefore this sample in general, has the potential for being biased. At present tag and jaw returns from non-bounty hunters can not be satisfactorily separated from bounty hunter returns.

Jaw Only Returned

This group of returns has the least potential for bias. Any individual who kills a grey seal, or finds a grey seal carcass, and goes to the trouble of removing the lower jaw is very likely to remove the tag and send it in with the jaw. Jaws received without tags are assumed to represent untagged animals.

Resident Populations and Emmigrants

Following the tagging operation some proportion of all tagged individuals leave Sable Island and become available to recapture. At

present there is no firm estimate of what proportion of a marked cohort remains as residents in and around Sable Island. These individuals are not available to recapture and do not mix with the unmarked population (the only exceptions being those caught by fishing gear deployed around the island). Obtaining estimates of this resident proportion would aid in determining the actual numbers of marked animals which are released to the total population each year. If these estimates were available on a yearly basis it would be possible to correct the number of marks in the population to account for those remaining in and around Sable Island. They are not as yet available.

A second group of animals which are only sporadically available for recapture are those which spend extended periods in a pelagic existence utilizing the offshore fishing banks. These are only captured on a chance basis by fishing gear.

Of the pups which do not take up residence on Sable Island or which do not remain pelagic, some proportion become mixed with unmarked animals born on other breeding sites and become available for recapture. These animals utilize inshore or near shore waters as feeding grounds and thus come into contact with a wide variety of human activities. Of all these marked animals a certain proportion go to the coasts of Newfoundland, Labrador, and U.S.A. From past assessments it has become apparent that these returns consist only of tagged animals. In Newfoundland and Labrador this situation appears to be due to either a lack of knowledge on the part of the fishermen, and other residents of rural communities, regarding the bounty payments or the absence of bounty payments. In the U.S.A. the animals are protected by law. At present we have not been able to deal with these data effectively and have merely excluded all Newfoundland returns from any further calculations. The numbers of marks excluded in this manner are given in Table 4. What effects this may have on the validity of the abundance estimates remains undetermined.

In summary this discussion of the assumptions of the present model indicate:

- 1) Marked animals do not appear to suffer a different rate of mortality than unmarked animals.
- 2) Examination of y_i (the proportion of marks in the total sample removed at time i) for the recapture series does not indicate a consistent trend. This implies that marked and unmarked animals experience equal rates of mortality over time.
- 3) Tag loss is assumed to be 10%.
- 4) Marked and unmarked animals do not appear to mix randomly during their first year of life as indicated by the distribution of ratios of marked to unmarked animals. These ratios become less patterned at age 1 indicating better mixing at older ages.
- 5) Bounty returns are least vulnerable to inflated numbers of marks.

Pup Production Estimates

Given the preceding caveats and considerations it was concluded that the bounty return data of animals aged 1 and older, represents the most reliable source of information on the distribution of marks in the populations. It appears to be the least vulnerable to inflated estimates of the numbers of marks and contributes samples from a relatively large portion of the grey seals' total range. The data set excludes; all returns from Newfoundland, Labrador, and U.S.A., and all tag only returns. Since these totals were excluded from the actual recapture trellis they were also removed from M_0 (the number of animals initially marked in the cohort) and n_i (the total returns at age during the i th interval). The resulting returns at age and the accompanying recapture trellis are given in Tables 5 and 6. These data are hereafter referred to a Series I. The calculations of \hat{N}_0 from these data are given in Appendix I. The results of the initial calculations in terms of numbers of pups produced are given in Table 7.

Population Estimates

Given the pup production estimates calculated in the previous section it remains to calculate total population size. This was achieved by utilizing the information on population age structure derived from the bounty kill samples given in Table 3. The numbers shot in each age group for 1979 and 1980 were combined to form a single vector of numbers at age. These years were chosen because information on the detailed age structure of individuals of age 20+ was available, and ages were read by one reader for consistency between years. The resulting vector is shown in Table 8. An exponential decay of the form;

$$\ln N_x = 5.009 - 0.127 x \quad (R^2 = 0.93),$$

described these data indicating a mortality rate (Z) of 0.127 for ages 1 and above. There was no conclusive evidence to indicate that Z for ages other than 0+ should be higher as was assumed by Harwood and Prime (1978) or Harwood (1981) (see Figure 4). This relationship translates into a survival rate of 0.88 for ages 1 and above. Mortality of pups is higher mainly due to the initial mortality from birth to weaning. Observations made during the whelping season on Sable Island indicate that mortality from birth to weaning is 20% (minimum estimate) ($Z = 0.20$, $S = 0.82$). Since we have no reliable estimate of mortality between weaning and age 1 we assume it equal to adult mortality, resulting in a survival in the first year of 0.82×0.88 or 0.72.

We combined these estimates of mortality rates with the vector of age specific pregnancy (Table 9) to define a transition matrix as described by Leslie (1945) of the form;

$$M = \begin{bmatrix} f_0 & f_1 & f_2 & f_3 & \dots & f_{k-1} & f_k \\ S_0 & 0 & 0 & 0 & \dots & 0 & 0 \\ 0 & S_1 & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & S_2 & 0 & \dots & 0 & 0 \\ \cdot & \cdot & \cdot & \cdot & \dots & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \dots & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \dots & \cdot & \cdot \\ 0 & 0 & 0 & 0 & \dots & S_{k-1} & 0 \end{bmatrix}$$

where $f_{0-3} = 0$, $f_4 = 0.08$, $f_5 = 0.355$, $f_{6-k} = 0.425$, and $S_0 = 0.72$ and $S_{1-k} = 0.88$.

Using these values assumes that the population is stationary. If we allow a population of 100 age 0+ (cast as a column vector) to grow according to this model we attain a stable age distribution as indicated in Table 10A. Since the NW Atlantic grey seal population appears to be increasing it is more realistic to adjust the values of S_x to account for the intrinsic rate of population increase. The only firm estimate of population increase comes from the Sable Island (Figure 5) colony which is increasing at 12% per year ($y = 318 e^{0.12x}$, $R^2 = 0.98$). This rate is approximately double the rate of increase estimated for the British grey seal populations (6-7% per annum) in Summers (1978). There is some evidence to indicate that the Sable Island rate of increase is somewhat inflated by the immigration of Gulf born breeders. Lacking other evidence to justify the 12% annual increase a rate of 7% per annum was assumed. This changes the subdiagonal of the transition matrix to $S_0 = 0.77$ $S_{1-k} = 0.95$. The stable age distribution achieved with this form of growth is given in Table 10B. From the resulting estimates of population age structure we can calculate total population numbers given the estimates of pup production calculated in the previous section. Using the 1978 pup production estimate as a reference point and the transition matrix defined above total grey seal population size for each of the years 1977 to 1983 were calculated (Table 11). This translates to a 1+ population size of between 71,000 and 125,000 in 1983.

These estimates of population size must be interpreted in light of the uncertainties involved in the data used in their calculation. To a certain extent these uncertainties are reflected in the extremely wide confidence intervals, but these do not account for all the uncertainties inherent in the calculations. Tag loss was assumed to be constant for each year, it may will be highly variable and of a larger or smaller magnitude than assumed here. The assumption of random mixing, partially met by excluding the younger ages is still not fully satisfied. The effect of violating this assumption on estimates of \hat{N}_0 is not known. Other assumptions made about the data are discussed above but their effects on the final estimates

of population size remain unknown. Until these can be investigated in more detail these estimates of population size should be viewed as best estimates given the present data. Caveat emptor.

Literature Cited

- Boness, J. and H. James. 1979. Reproductive Behavior of the Grey Seal (Halichoerus grypus) on Sable Island, Nova Scotia. *J. Zool. London* (1979) 188, 477 - 500.
- Bowen, W.D. and D.E. Sergeant. 1983. Mark-Recapture Estimates of Harp Seal Pup (Phoca groenlandica) Production in the Northwest Atlantic. *Can. J. Fish. Aquat. Sci.* 40: 728 - 742.
- Burton, R.W., Anderson, S.S., and C.F. Summers. 1975. Perinatal Activities in the Grey Seal (Halichoerus grypus). *J. Zool. (London)* 177(2), 197 - 201.
- Fogden, S.C.L. 1968. Suckling Behaviour in the Grey Seal (Halichoerus grypus) and Northern Elephant Seal (Mirounga angustirostris). *J. Zool. (London)* 154, 415 - 420.
- Fogden, S.C.L. 1971. Mother-young Behaviour at Grey Seal Breeding Beaches. *J. Zool. (London)* 164, 61 - 92.
- Harwood, J. 1981. Managing Gray Seal Populations for Optimum Stability. In, *Dynamics of Large Mammal Populations*, C.W. Fowler, Ed. Publ. by J. Wiley and Sons Inc. Pages 159 - 172.
- Harwood, J. and J.H. Prime. 1978. Some Factors Affecting the Size of British Grey Seal Populations. *Journal of Applied Ecology* (1978), 15, 401 - 411.
- Hewer, H.R. 1964. The Determination of Age, Sexual Maturity, Longevity, and a Life-table in the Grey Seal (Halichoerus grypus). *Proc. Zool. Soc. London.* 142(4), 593 - 624.
- Laws, R.M. 1953. A New Method of Age Determination for Mammals with Special Reference to the Elephant Seal. Mirounga leonina Linn. *Sci. Rep. Falkland Is. Dep. Surv. No. 2*, 1 - 11.
- Leslie, P.H. 1945. On the use of Matrices in Certain Population Mathematics. *Biometrika*, 33, 183 - 212.
- Mansfield, A.W. and B. Beck. 1977. The Grey Seal in Eastern Canada. Technical Report #704 of the Canadian Dept. of Fisheries and the Environment.
- Seber, G.A.F. 1982. The Estimation of Animal Abundance and Related Parameters. 2nd Ed. Publ. by Charles Griffen & Co. Ltd. London. Pages 125 - 129.
- Summers, C.F. 1978. Trends in the Size of British Grey Seal Populations. *J. Applied Ecology*, (1978) 15, 395 - 400.

- Paloheimo, J.E. 1963. Estimation of Catchabilities and Population Sizes of Lobsters. J. Fish. Res. Bd. Canada 20, 59 - 88.
- Zwanenburg, K., B. Beck, and S.J. Smith. 1981. Eastern Canadian Grey Seal (Halichoerus grypus) Research Report and 1980 Stock Assessment. Canadian Atlantic Fisheries Scientific Advisory Committee Research Document 81/81.

Table 1. Age distributions of collector killed samples.

Age	1968	1969	1970	1975	Total 1968-1975	1982**
0	10	46	110	30	196	41
1	2	6	28	19	55	53
2	5	10	28	17	60	11
3	9	11	28	8	56	10
4	7	9	21	16	53	7
5	6	11	19	8	44	10
6	0	7	15	5	27	3
7	4	4	4	3	15	4
8	4	8	8	1	21	4
9	2	7	2	3	14	3
10	4	6	8	0	18	5
11	2	1	6	1	10	5
12	1	3	8	0	12	3
13	1	0	2	0	3	4
14	0	1	2	1	4	6
15	1	1	1	1	4	3
16	0	1	0	1	2	1
17	8*	8*	15*	4*	5	5
18	-	-	-	-	3	5
19	-	-	-	-	3	2
20	-	-	-	-	4	2
21	-	-	-	-	20	21
Total 1+	56	94	195	88	433	167
Total 0+	66	140	305	118	629	208

*Indicates that these include animals older than 17.

**These animals are included in the 1982 bounty kill sample.

Table 2. Controlled cull¹.

Year	Males	Females	Total Adults ²	Pups	Total
1967	14	3	17	212	229
1968	16	2	18	134	152
1969	3	19	189	589	778
1970	-	-	125	520	645
1971	-	-	122	743	865
1972	22	110	132	599	731
1973	4	35	64	558	622
1974	17	109	126	1042	1168
1975	54	480	534	1619	2153
1976	13	83	96	545	641
1977	150	192	342	1046	1388
1978	59	88	147	569	716
1979	15	30	45	269	314
1980	46	165	211	921	1132
1981	119	277	396	1212	1608
1982	140	578	718	1009	1727

¹ Includes seals killed by others and found during the cull.

² Not all adults are sexed so the total may be different from males plus females.

Table 3. Age distributions of bounty kill samples.

Age	1976	1977	1978	1979	1980	1981	1982
0	188	202	363	420	408	362	125
1	51	29	63	133	84	73	82
2	66	31	17	51	56	62	26
3	53	30	33	26	45	47	23
4	61	24	9	28	20	23	25
5	48	32	22	22	26	10	22
6	45	31	14	29	25	11	10
7	26	27	15	32	31	15	12
8	35	32	17	23	28	9	13
9	16	24	9	29	30	10	8
10	16	19	7	23	23	6	10
11	24	19	9	21	21	12	10
12	18	16	14	18	25	15	16
13	7	16	5	14	15	13	12
14	14	15	10	9	23	7	15
15	13	10	3	13	10	5	12
16	14	11	3	13	10	11	9
17	5	8	14	13	9	5	10
18	4	6	3	8	9	3	9
19	5	5	2	4	10	5	9
20	5	5	3	0	6	5	5
21+	20	21	15	32	38	26	33
Total 0+	734	613	650	961	952	735	496
Total 1+	546	411	287	541	544	373	371

Table 4. Numbers of marks returned from Newfoundland, Labrador, and U.S.A.

Cohort	i =	1	2	3	4	5
1977		15	2	1	0	0
1978		31	1	2	0	
1979		37	2	0		
1980		35	6			
1981		22				

Table 5. Total returns at age for Series I. Each total consists only of bounty returns from Sable cohort and Gulf cohorts.

Year	0	1	2	3	4
1977	202	63	51	45	23
1978	363	133	56	47	
1979	420	84	62		
1980	408	73			
1981	362				

Table 6. Numbers of marks recaptured via the bounty kill from cohorts marked on Sable Island and in the Gulf of St. Lawrence. These data were used as input for Series I estimates of \hat{N}_0 .

M_0	Cohort	$i =$	1	2	3	4	5
1885	1977		6	2	9	6	3
2189	1978		32	28	7	8	
3066	1979		84	17	10		
3332	1980		40	4			
2764	1981		35				

Table 7. Values of N_0 as calculated from recapture data presented in Tables 5 and 6. Recaptures from the 1st interval (age 0) were excluded and M_0 was adjusted to account for tag loss (see Appendix I)*.

Year	\hat{N}_0	Cull	Pup Production	95% Confidence Limits
1977	14779	1046	15825	11026 - 24904
1978	10611	569	11180	8596 - 15135
1979	14485	269	14754	10521 - 21986

* The 1980 value was excluded since it was based on only one year of returns.

Table 8. Numbers at age from 1979 and 1980 bounty kills.

Age	Numbers
1	217
2	107
3	71
4	48
5	48
6	54
7	63
8	51
9	59
10	46
11	42
12	43
13	29
14	32
15	23
16	23
17	22
18	17
19	14
20	6
21	19
22	7
23	8
24	4
25	7
26	6
27	5
28	2
29	4
30	2
31	0
32	1
33	0
34	2
35	1
36	1
37	0
38	1

Table 9. Pregnancy rates for females grey seals from Mansfield and Beck 1977.

Age	Percent Pregnant
0	0
1	0
2	0
3	0
4	0.16
5	0.71
6	0.85
7	0.85
8	0.85

Table 10. Stable age distributions obtained from the Leslie Matrix model of population growth. A = assumes a stationary population; B = assumes a population with an intrinsic rate of increase of 7% per year. See text for details.

A Stationary Population Percent at Age		B Increasing Population Percent at Age	
Age		Age	
0	17.8	0	17.0
1	12.3	1	12.1
2	10.5	2	10.3
3	8.9	3	8.8
4	7.6	4	7.5
5	6.4	5	6.4
6	5.5	6	5.5
7	4.7	7	4.7
8	4.0	8	4.0
9	3.4	9	3.4
10	2.9	10	2.9
11	2.4	11	2.5
12	2.1	12	2.2
13	1.8	13	1.9
14	1.5	14	1.6
15	1.3	15	1.4
16	1.1	16	1.2
17	0.9	17	1.0
18	0.8	18	0.9
19	0.7	19	0.7
20	0.6	20	0.6
21	0.5	21	0.5
22	0.4	22	0.5
23	0.4	23	0.4
24	0.3	24	0.3
25	0.3	25	0.3
26	0.2	26	0.2
27	0.2	27	0.2
28	0.2	28	0.2
29	0.1	29	0.2
30	0.1	30	0.1
31	0.1	31	0.1
32	0.1	32	0.1
33	0.1	33	0.1
34	0.1	34	0.1
35	0.1	35	0.1
		36	0.1

Table 11. Estimates of the total number of grey seals (including pups) derived from estimates of pup production and age distributions calculated from the Leslie model.

Year	Total Population Size	95% Confidence Limits
1977	59055	45412 - 79943
1978	65675	50504 - 88904
1979	73028	56157 - 98854
1980	81198	62433 - 109908
1981	90276	69411 - 122205
1982	100366	77178 - 135867
1983	111601	85809 - 151068

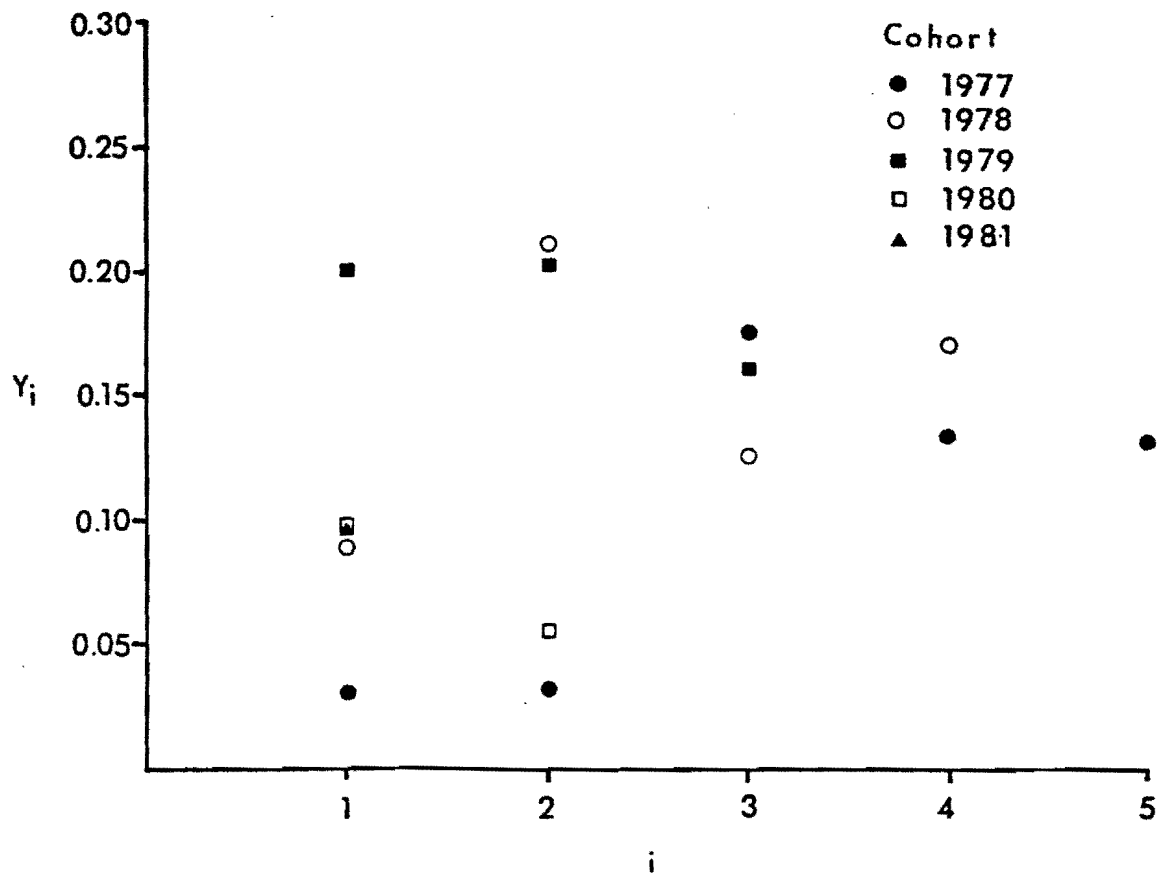


Figure 1. Values of Y_i versus i for all cohorts.

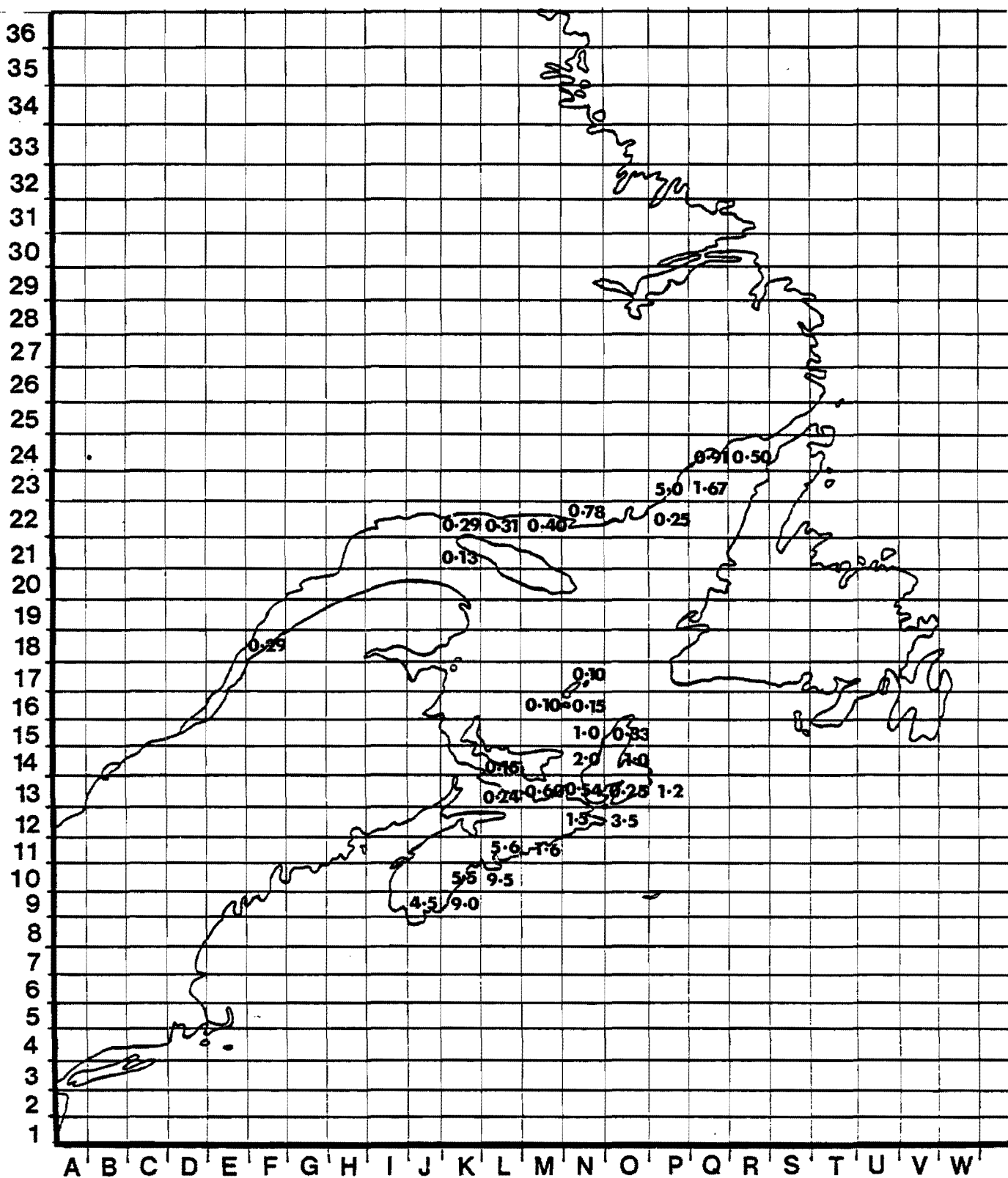


Figure 2. Distribution of the ratio of tagged to untagged grey seal pups (age 0⁺). Calculated from cumulative values 1977 to 1980.

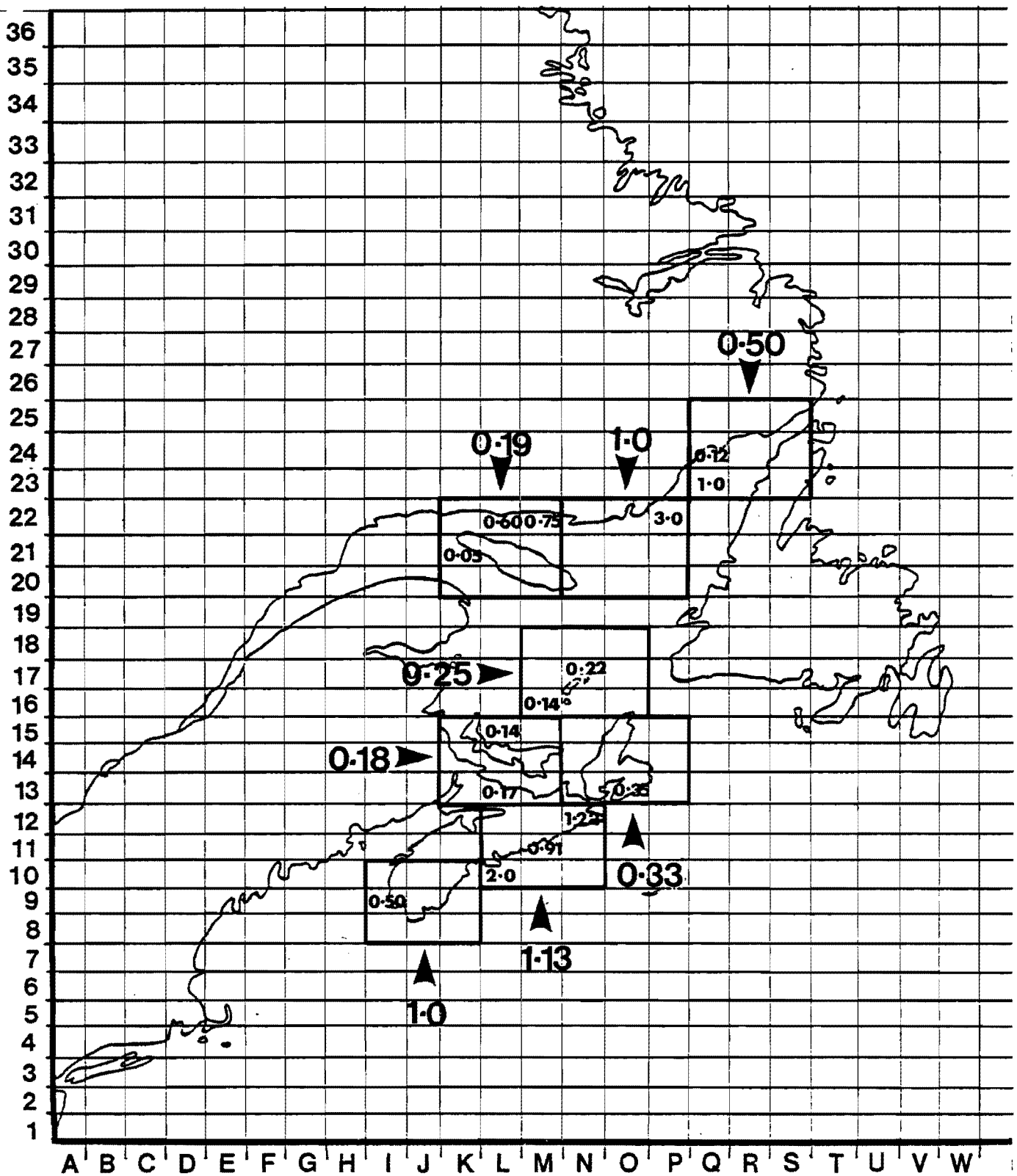


Figure 3. Distribution of the ratio of tagged to untagged grey seals (age 1⁺). Calculated from cumulative values 1977 to 1980.

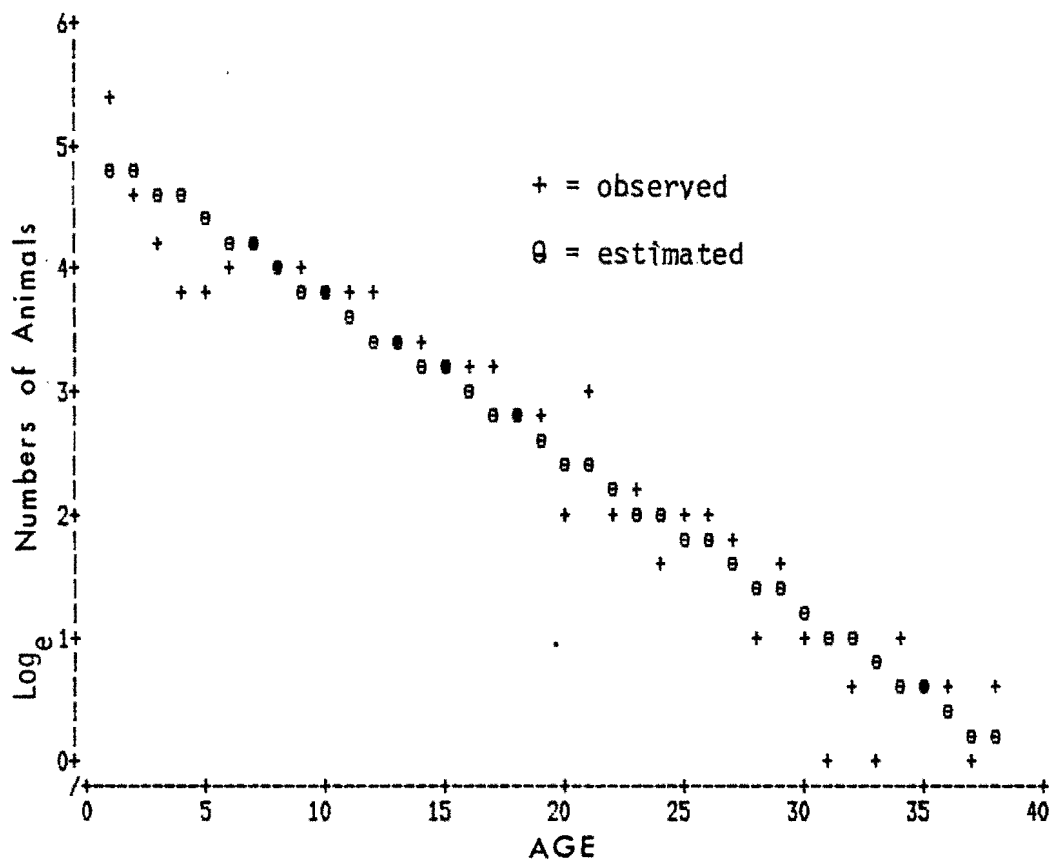


Figure 4. Log_e numbers observed at age (N_x) in the 1979 and 1980 bounty samples plotted against age ($\ln N_x = 5.009 - 0.127 X$ $R^2 = 0.93$).

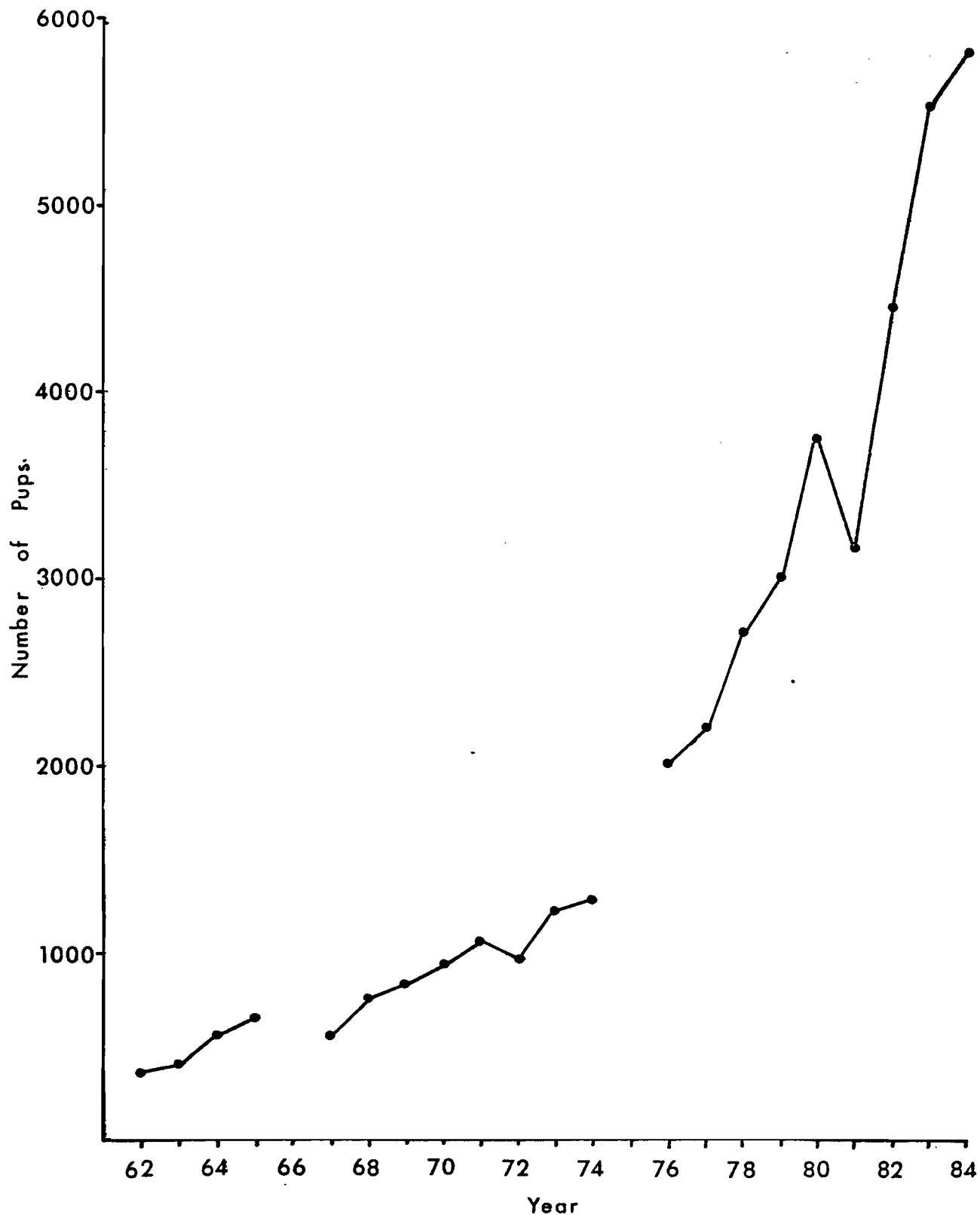


Figure 5. Pup production on Sable Island, Nova Scotia, since 1962. Data partly from Mansfield and Beck (1977) and from actual counts in later years.

Appendix I. Calculations of \hat{N}_0 using data from Series I - bounty returns only.

1977 Cohort

i	m_i	n_i	y_i	
(1	6	202	0.0297)*	$M_0 = 1885-188 = 1696^{**}$
2	2	63	0.0317	$\hat{N}_0 = 14779^+$
3	9	51	0.1765	95% CL = 9980-23858
4	6	45	0.1333	
5	3	23	0.1304	
	20	182		

1978 Cohort

i	m_i	n_i	y_i	
(1	32	363	0.0882)*	$M_0 = 2189-219 = 1970$
2	28	133	0.2105	$\hat{N}_0 = 10611$
3	7	56	0.1250	95% CL = 8027-14566
4	8	47	0.1702	
	43	236		

Appendix I. Cont'd

1979 Cohort

i	m_i	n_i	y_i	
(1	84	402	0.2000)*	$M_0 = 3066-307 = 2759$
2	17	84	0.2024	$\hat{N}_0 = 14485$
3	10	62	0.1613	95% CL = 10252-21717
	27	146		

1980 Cohort

i	m_i	n_i	y_i	
(1	40	408	0.0980)*	$M_0 = 3332-333 = 2999$
2	4	73	0.0548	$\hat{N}_0 = 44385$
	4	73		95% CL = 21249-142409

* Indicates that these returns were not utilized in the calculation of \hat{N}_0 due to the patterned distribution of returns (see discussion under "Mark Recapture Model Employed").

** Values of M_0 adjusted for tag only returns, returns from Newfoundland, Labrador, USA, and 10% tag loss.

+ \hat{N}_0 calculated using $\hat{N}_0 = M_0 (\sum n_i) + 1 / (\sum m_i) + 1$