

**stichting
mathematisch
centrum**



AFDELING TOEGEPASTE WISKUNDE
(DEPARTMENT OF APPLIED MATHEMATICS)

TN 101/81

AUGUSTUS

E. FLIPSE & E.J.M. VELING

AN APPLICATION OF THE LESLIE MATRIX MODEL TO THE
POPULATION DYNAMICS OF THE HOODED SEAL
(*CYSTOPHORA CRISTATA* ERXLEBEN)

kruislaan 413 1098 SJ amsterdam

Printed at the Mathematical Centre, 413 Kruislaan, Amsterdam.

The Mathematical Centre, founded the 11-th of February 1946, is a non-profit institution aiming at the promotion of pure mathematics and its applications. It is sponsored by the Netherlands Government through the Netherlands Organization for the Advancement of Pure Research (Z.W.O.).

An application of the Leslie matrix model to the population dynamics of the Hooded Seal (*Cystophora cristata* Erxleben)

by

E. Flipse & E.J.M. Veling

ABSTRACT

In order to investigate the stability of the Hooded Seal population near the island Jan Mayen the Leslie matrix model has been used. The influence of the hunt has been incorporated by rescaling the parameters. This leads to solving a nonlinear eigenvalue problem; the results suggest that the hunting pressure is equal to or just more than the population can stand.

KEY WORDS & PHRASES : *population dynamics, Leslie matrix*

1. INTRODUCTION

In recent time there has been arisen a real concern about the stability of the zoological resources of the North Atlantic. By the traditional hunting of the coastal inhabitants of Norway and Canada the very large populations of the Harp Seal (*Pagophilus groenlandicus* Erxleben) and the Hooded Seal (*Cystophora cristata* Erxleben) have been heavily reduced.

In order to study the population dynamics of the last species the first author has accompanied Norwegian seal hunting expeditions to the "West Ice" (Vesterisen") breeding area near the island Jan Mayen for several years. It was possible on these trips to collect material for age determination from adult Hooded Seals. In this paper use will be made only of the 1975 sample. That year was the most succesful: it resulted among other things in the collection of 259 lower jaws and skulls of adult females. Together with the second author a mathematical model was set up. Here we report on our analysis.

The first author, Eric Flipse, died in a tragic accident taking place in Afghanistan in August 1979. The second author completed the analysis of his collected data.

2. MATERIAL AND METHOD

The Hooded Seal is a medium-sized member of the Phocinae and inhabits the North Atlantic and the Atlantic portion of the Arctic Ocean, where it can be found on floating ice. The species prefers deep waters and is rarely seen on land or on solid coastal ice. Most Hooded Seals are usually born between March 10th and March 20th, and in this period the hunters assemble at the breeding grounds. For more information about the biology of the Hooded Seal and the history and present status of the population we refer to Sergeant (1976).

The material collected during the expeditions to the "West Ice" has been analyzed by the first author at the Institute for Taxonomic Zoology, University of Amsterdam, see table 1. One of the lower canines of each animal was used for age determination. Using a Buehler Isomet low speed saw equiped with a diamond wafering blade, a longitudinal section

(approximately 90-120 μ thick) was cut. No staining was applied. The section was glass mounted and examined with a Wild M5 stereomicroscope. Transient light (polarized) was found to be suitable. The age was determined according to the annual layers visible inside the neonatal line and the number of annual layers in the cementum. A detailed technical description is available upon request. This ageing technique for pinnipeds has been described by several authors (e.g. Laws 1962).

age	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
# $\frac{00}{++}$	0	15	25	39	41	31	17	17	12	15	10	6	5	2	1
age	18	19	20	21	22	23	24	25	26	27	28	32	34	Σ	
# $\frac{00}{++}$	5	1	2	3	2	3	1	1	1	1	1	1	1	259	

Table 1. Age distribution of the 1975 sample collected at MV "Polaric"

The most obvious way to study the status of a population is to use the year class backtracking model. However a long series of statistics is necessary, so its usefulness is quite restricted in general. Recently Jacobsen (1979) using all possible information has done that work for the Hooded Seal. Another possibility is to use the Leslie matrix model, which is simple but in order to apply one needs the knowledge of the value of some parameters which are difficult to assess. We used the last method where we have taken the value of the parameters both from Øritsland & Benjaminsen (1975a) and from the more updated study of Jacobsen (1979).

In section 3 we discuss the year class backtracking model and in section 4 we apply the matrix analysis. A way is suggested to treat the absolute numbers of the catch into a relative model as the Leslie one. In section 5 we discuss the results.

3. DISCUSSION OF THE YEAR CLASS BACKTRACKING MODEL

The best possible calculation or estimation of vital population statistics is necessary when information on the population state is desired for possible management programmes. These vital statistics include

parameters such as (age specific) mortality and reproduction rates, age frequencies, production and population size.

Several techniques and methods are available for determining such parameters, but their usefulness for a population study depends largely on the practical possibilities of the population concerned. The simplified diagram in fig. 1 illustrates some possible methods and combination of methods for the ice-breeding Hooded Seal.

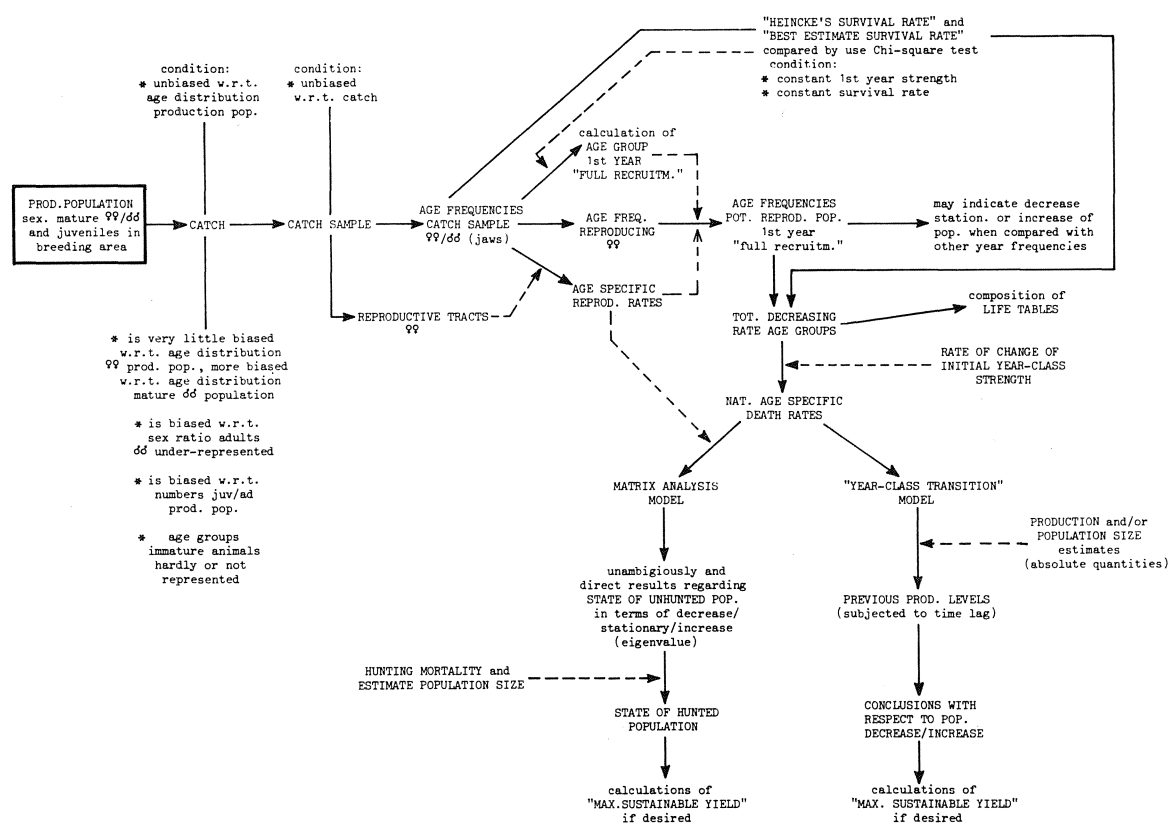


Fig 1. Scheme for study of the population dynamics of the Hooded Seal

These methods are based on 3 main techniques:

1. Information derived from direct counting of animals in the breeding and /or moulting areas by means of aerial photography.
2. Information derived from a tag-recovery programme.
3. Information derived from catch samples and catch curve analysis.

All the three methods should preferably be used and the results compared.

As far as the "West Ice" Hooded Seal population is concerned the methods of aerial survey and tag-recovery have serious practical disadvantages (e.g. bad weather conditions; breeding area far away from inhabited land masses resulting in the need for costly long-range aircraft; tag-recovery programmes can be applied crudely only: the period for pup tagging is very limited). Hence almost all information on the "West Ice" Hooded Seal population, including that presented in this paper, has derived from catch samples and from observations done (mostly) on commercial sealing vessels.

The main variables responsible for a certain population state are the number of animals added to (production) or subtracted from (mortality, catch) the closed population during a certain period of time. It is easy to find a relation between the total numbers of individuals at a certain age, the size of the population at the time these individuals were born, natural survival rate and catch which these individuals have been subjected to, by the following reasoning. Define

- $P_{n,y+n}$ = number of seals having age n in year $y+n$
(i.e. the number of animals born in year y and still alive in year $y+n$).
- B_y = production in year y ; initial yearclass; original strength of age group n in year $y+n$.
- $C_{n,y}$ = catch, number of animals aged n , caught in year y .
- s_n = natural survival rate for animals of age n after catch in year $y+n$, but before the following year's hunt (i.e. year $y+n+1$).

Hence, the number of survivors aged n in year $y+n$ ($P_{n,y+n}$) were born in year y and are part of that year's production B_y . The year class born in year y (B_y) will be decreased during the hunting season by a pup catch $C_{0,y}$, and

the number of animals which survive up to the 2nd hunting season (year $y+1$) will be $P_{1,y+1} = (B_y - C_{0,y}) s_0$. Repeating this reasoning we arrive at the following formula

$$P_{n,y+n} = (\dots(B_y - C_{0,y}) s_0 - C_{1,y+1}) s_1 - \dots - C_{n-1,y+n-1}) s_{n-1}$$

and we can express B_y as follows

$$B_y = (\dots(P_{n,y+n}/s_{n-1} + C_{n-1,y+n-1})/s_{n-2} + \dots + C_{1,y+1})/s_0 + C_{0,y}.$$

This equation represents a model usable for "backtracking" provided a series of hunting statistics: parameters such as natural mortality, age frequency and population size at a certain time, are known or can be estimated.

Basically, this model describes the history of a certain year class during some years. When the same technique is applied to other year classes represented in the age sample, a picture of the reproductive performance of the breeding population can be obtained by calculating the production sizes during a range of years. Hence an indication of the state of the population (increasing, stationary or decreasing), during a period up to about 6 years prior to the time of the age sample used as a basis for the analysis, becomes available.

When this "year class" model is used no conditions concerned with the stability of the population need to be met. However, in practice these will usually have to be considered in order to estimate s_n (the natural survival rate) and/or in cases where only a few age samples are available. Several quantities in the model are of an absolute nature. This can be considered to be a disadvantage as absolute figures for production and population size are difficult to arrive at. When an assessment of the population, in terms of increase or decrease, has to be made, absolute values of population and/or production size ($P_{n,y+n}$ and B_y) must be known or estimated.

A further disadvantage of this model is the impossibility of making a direct population assessment both in terms of time and in terms of dealing with the population as such (year class model). Hence, this method does not reveal the immediate population state in terms of increase or decrease at the time of the investigation (year of last available age frequency) nor the

5-6 preceding years. The direct results arrived at by this model refer to occasions in the past. A 5-6 year time lag is inherent to this model as a certain year class is subjected to backtracking so the period between birth and "first year full recruitment age" will be encountered in the age sample. However, sometimes it might be possible to estimate mean production levels between the time of investigation and the 5-6 years prior to this, provided information on the production size during the year of investigation can be derived from other sources.

Finally, a serious drawback of this model, when assessing a decrease or increase trend, is the need for a considerable number of age frequency samples. See Jacobsen (1979). When backtracking many year classes represented in a normal age sample a period of some 10-15 years should be covered. However, when such an extensive range of age frequencies is unavailable this requirement can be met by introducing more simplifications. If one assumes the year class distribution not to be subjected to big changes during the period concerned, the mean year class distribution can be applied.

4. APPLICATION OF MATRIX ANALYSIS

4.1. Introduction

Another approach for establishing a mathematical population model is to calculate the transition of the breeding population from year N to year $N+1$ using probabilities. A matrix frame work for such a population model is very useful since it allows easily the study of the influence of the parameters (birth and death rates, age distribution at a given time) on the population structure in later years. This discrete deterministic form of population analysis based on matrix analysis was introduced among others by Leslie (1945). A readable account of this method can be found in Pielou (1969, Chapter 3). We shall modify this method a little bit in such a way that we try to take into account the influence of the hunting pressure on the population.

A feature of the matrix model is that there is no need of absolute quantities for determination of the state of the un hunted population in terms of increase or decrease. Based on information of the birth and death rates we obtain a picture which reflects the state of the population at the time

of investigation and afterwards we can compare the calculated age distribution under the assumption that the hunt is of minor importance with the age distribution we find in a sample. But, since this last assumption is not right, we have to modify our method in such a way that we incorporate the absolute catch figures into the relative death rates. This will be done by expressing the catch figures as fraction of the total population: hence the total population size has to be known or estimated, which in the case of the "West Ice" Hooded Seal population represents a serious problem. But in any case this estimate is easier than to determine the quantities $C_{n,y}$ for a number of years when we use the "backtracking" model.

For application of the matrix analysis in case of hunting it is necessary to assume that the age distribution differs not too much from the so-called stable age distribution, which notion we shall explain later. Finally we remark that age specific reproduction and natural survival rates are usually derived from a hunted population, so we might expect that these values, in particular the reproduction rates, differ somewhat from those prevailing in a population which is not hunted.

Only the female portion of the breeding population will be investigated in this paper and the assumption is made that the state of the female breeding population reflects the state of the breeding population as a whole. This assumption is based on:

1. Hooded Seals assemble in scattered groups of families consisting of a (nursing) female and dog. The dog awaits the time of weaning after which mating takes place and the animals disperse. Observations suggest a monogamous behaviour.
2. Differences in hunter avoidance behaviour in the breeding area cause females to be subjected to considerably greater hunting pressure than males. This probably has resulted in a male surplus in the breeding area. Sometimes 2 or even 3 males are seen competing for a single female. These surplus probably do not significantly influence the reproductive performance of the female breeding population. However, further and prolonged disturbance of the sex ratio could possibly lead to a reduced production.
3. Age frequencies derived from a female catch are the least biased on account of the hunter avoidance behaviour and the first year full

recruitment (being at 6 years of age). The first year full recruitment in the male may be as high as 14 years.

The state of a hypothetical unhunted Hooded Seal population will first be considered using knowledge of age composition, age specific reproduction and natural death rates. The consequences of the hunting will then be investigated.

4.2. Matrix frame-work

We consider the following female age classes: 0-1, 1-2, ..., 10-11, and finally 11 years and older and we describe the evolution of the population from year N to $N+1$. Define

x_n = the number of females (aged n) just after the weaning period and in the case of hunting the number of surviving females (aged n) just after the hunting period.

Hence x_0 is the number of surviving female pups after the first hunting season to which they are subjected just after their birth. The age classes concerned are thus: x_0, x_1, \dots, x_{10} and finally x_{11} , where x_{11} represents the combined year classes 11 and older. To be able to compare year classes from different initial years the number of females aged n surviving the hunting season in year N will be denoted as x_n^N . By \underline{x}^N we mean the column-vector, consisting of the numbers (x_0^N, \dots, x_{11}^N) , and we call it the *population vector*.

The evolution of the population from year N to year $N+1$ can now be computed using probability rates and can be written in a matrix frame-work as follows: $\underline{x}^{N+1} = M \underline{x}^N$, where $M = (a_{ij})_{i,j=0}^{11}$ is the corresponding so-called Leslie matrix. To make this more explicit, we can also write

$$x_i^{N+1} = \sum_{j=0}^{11} a_{ij} x_j^N, \quad i = 0, \dots, 11.$$

The greater part of the elements of M are zero, except for the following

$$a_{0j}, \quad j = 2, \dots, 11,$$

$$a_{i+1,i}, i = 0, \dots, 10, \text{ and } a_{11,11}.$$

We introduce the following numbers:

r_n = age specific reproduction rate of females whelping a pup at age n , $n = 3, \dots, 11$.

s_n = natural age specific survival rate of females at age n , $n = 0, \dots, 11$.

Now we specify the nonzero elements of the matrix M , see Pielou (1969):

$$a_{0j} = \frac{1}{2} r_{j+1} s_j, \quad j = 2, \dots, 10,$$

$$a_{0,11} = \frac{1}{2} r_{11} s_{11},$$

$$a_{i+1,i} = s_i, \quad i = 0, \dots, 10,$$

$$a_{11,11} = s_{11}.$$

The factor $\frac{1}{2}$ turns up because we consider only the female population. The matrix M consists of nonzero elements on the first row, except for the first two and further on the lower subdiagonal and in the lower right corner.

We can interpret the numbers of the column-vector as the absolute numbers of the respective year classes, but also as the relative frequency of the respective year class in the population with respect to a given year class, let us say x_0 , if we divide all numbers by x_0 . In that case we call the vector \underline{x}^N the *age frequency vector*, and we denote it by $\hat{\underline{x}}^N$. In this form the matrix treatment is independent of the total size of the population, as far as it is not logical to study very small populations in this way, in view of the restrictions put by the use of survival rates and reproduction rates, which is based on probability arguments. By very small populations the effect of random events will seriously affect the computed evolution.

We want to derive some quantitative information about the state of the population from this matrix. Especially we are interested in the value λ such that $\underline{x}^{N+1} = M \underline{x}^N = \lambda \underline{x}^N$, which means $x_i^{N+1} = \lambda x_i^N$, $i = 0, \dots, 11$. If the population vector \underline{x}^N fulfils this requirement, we call \underline{x}^N the

eigenvector belonging to this eigenvalue λ . This eigenvalue is a solution of the equation $\det (M-\lambda I) = 0$ and is real and positive. The corresponding eigenvector consists of real positive numbers. We call the corresponding age distribution *stable*, because in this case the vectors \hat{x}^N and \hat{x}^{N+1} (i.e. x^N and x^{N+1} after normalization) are the same. But it does not mean that the numbers of the population are equal in successive years. The population is increasing if $\lambda > 1$, decreasing if $\lambda < 1$ and stationary if $\lambda = 1$. For the special case $a_{11,11} = s_{11} = 0$ the corresponding matrix has the same form as in paper of Leslie (1945). Then it can be proved that there exists only one real positive eigenvalue λ_0 , all the others $\lambda_1, \dots, \lambda_{11}$ are either negative or complex, with the inequalities $|\lambda_0| = \lambda_0 > \lambda_1 \geq \dots \geq |\lambda_{11}|$. A further property of this matrix M is that the age distribution will converge after successive applications of the matrix M to the age distribution of the eigenvector belonging to λ_0 for any initial distribution, so the age distribution will look like the stable one (Leslie 1945). In our case $s_{11} \neq 0$; it is now possible that there arise one or more real positive eigenvalues, but the age distribution will still converge to the eigenvector of λ_0 if $\lambda_0 = |\lambda_0| > |\lambda_i|$, $i = 1, \dots, 11$. We encountered this case for the coefficients we have used in the matrix M .

4.3. Age specific reproduction rates, r_n

Øritsland (1975) obtained age specific reproduction rates in female Hooded Seals from Newfoundland by determining the percentage of *corpus luteum* shown in the reproductive organs collected. Assuming those values to be valid for other Hooded Seals populations as well we used them in our calculations, see table 2.

age i	3	4	5	6	7	8	9	10	11
rate r_i	0.118	0.556	0.716	0.826	0.935	0.944	0.944	0.960	0.980

Table 2. Age specific reproduction rates r_i according Øritsland (1975)

Recently Jacobsen (1979) obtained new data, see table 3.

age i	3	4	5	6	7	8	9	10	11
rate r_i	0	0.390	0.713	0.912	0.950	0.950	0.950	0.950	0.950

Table 3. Age specific reproduction rates r_i according Jacobsen (1979)

No indication could be detected for a decreasing reproductive performance in age groups over 11 years.

4.4. Age specific natural survival rates, s_n

Age specific natural survival rates have to be calculated from catch-curve analysis. The first year full recruitment age (i.e. youngest age group fully represented in the age frequency sample) and annual survival rate (i.e. combined effects of natural death rate and hunting pressure) may be extracted from the age frequency of a catch sample by use of the methods of Heincke (1913), Chapman & Robson (1960) and Robson & Chapman (1961). For an application of these techniques it is necessary that one can assume that the survival rates are constant (or at least over a limited range of year classes) and that the initial year classes are of equal strength. As it appears to be reasonable to expect different survival rates for immature (mostly unhunted, and therefore hardly represented in the sample) individuals and mature animals, which are part of the hunted population, two mean annual survival rates (for 0-2 years old and 3 years and older animals) are computed. But in the sequel we shall consider also the case of two survival rates (for 0 years old and 1 years and older animals) and the case of only one survival rate (for all animals the same).

As the West Ice Hooded Seal population has decreased during the last 10 years, the requirement of a constant initial year class recruitment can not be satisfied and a realistic adjustment has to be made. The first year full recruitment age in the sample is obtained by applying a chi-square test to the results of Heincke's "estimate of survival rate" and the "best estimate" formulated by Chapman and Robson. Now we specify both estimates: s_H (Heincke's estimate) and s_C (Chapman and Robson's estimate) for the survival rate of the 3 years and older seals. Define

n = the number of seals in the sample,

n_i = the number of seals of age i in the sample,

i_0 = the youngest age in the sample,

i_m = the oldest age in the sample,

$$T = \sum_{i=i_0}^{i=i_m} n_i (i-i_0),$$

then the estimates become

$$s_H = (n - n_{i_0})/n,$$

$$s_C = T/(n+T-1).$$

As it seems reasonable to exclude a sampling error, a possible discrepancy between s_H and s_C may be attributed to a deficiency in the youngest year class i_0 . It means that the youngest age group is underrepresented in the sample and not fully recruited in the breeding population. We assume a discrepancy if the corresponding test variable χ^2 satisfies $\chi^2 > 3.842$ with $P > 0.95$; see table 4 for χ^2 . In that case the test can be repeated by elimination of the youngest age group in the sample. Continuation of this process until the chi-square test yields no discrepancy, determines the first year full recruitment age. The results of this procedure applied to the 1975-sample (see table 1) are given in table 4. A first year full recruitment age of 6 years has been determined, which is the same as in the paper by Øritsland & Benjaminsen (1975a).

Sample 1975	$i_0 = 4$	$i_0 = 5$	$i_0 = 6$
s_C	0.846	0.828	0.813
s_H	0.942	0.898	0.822
$\chi^2 = \frac{(s_C - s_H)^2 n(n+T-1)^2 (n+T-2)}{T(T-1)(n-1)}$	21.87	10.06	0.135
	> 3.841	> 3.841	< 3.841

Table 4. Calculation of survival rates and determination of first year full recruitment age

Above we have calculated the survival rate under the assumptions of equal initial year classes and no hunting activities. We have to adjust the value found ($s = 0.822$) for these influences. The long term decrease (1960-1969) of the initial year classes influences the survival rate too

optimistic. From calculations done by Øritsland & Benjaminsen (1975a) the rate should be adjusted by a factor $s_y = 0.986$, which is equivalent to the calculated instantaneous natural mortality ($m_y = 0.014$) of the year classes. We remark that $s_y = \exp(-m_y)$. The result becomes $s = 0.811$. Finally we have to make corrections for the hunting activities. We shall calculate these corrections for three different hypotheses for the size of the breeding female population F , namely $F = 50000$, 70000 and 90000 . From the information given by Øritsland & Benjaminsen (1975a) there have been killed a number of 6500 female seals averaged during the years 1960-1969. The effect of the hunt has dropped the found survival rate. In table 5 we have made the adjustments for the three different choices for F .

Female breeding population F	50000	70000	90000
hunting pressure Q/F for $Q=6500$: p	0.130	0.093	0.072
survival rate with respect to the hunt: $s_I = 1-p$	0.870	0.907	0.928
survival rate corrected with respect to decreasing initial year classes: $s_{II} = 0.986 * 0.822$	0.811	0.811	0.811
natural survival rate: $s = s_{II}/s_I$	0.931	0.894	0.874

Table 5. Calculation of the natural survival rate

4.5. Age distribution without hunt

Now we fix the numbers s_n . Following the discussion above we put $s_n = s$, $n = 3, \dots, 11$, and we take for s the values from table 5 for the three different choices for F and the r_i - values from table 2. The survival rate for the youngest animals is difficult to assess. We make three options:

- (A) $s_0 = s_1 = s_2 = 0.85$;
- (B) $s_0 = 0.85$; $s_1 = s_2 = s$ (as Øritsland & Benjaminsen (1975)) ;
- (C) $s_0 = s_1 = s_2 = s$ (as Jacobsen (1979)).

By the special form of the matrix M it is possible to give an explicit representation of the eigenvector corresponding to the eigenvalue λ_0 . After normalization this vector takes the form $\underline{\hat{x}} = (\hat{x}_i)_{i=0}^{i=11}$, where

$$\begin{aligned}\hat{x}_0 &= 1, \\ \hat{x}_i &= \lambda^{-i} (s_0)^j (s)^{i-j}, \quad i = 1, \dots, 10, \quad j = \min(i, k), \\ \hat{x}_{11} &= \lambda^{-i} (\lambda - s)^{-1} (s_0)^k (s)^{11-k},\end{aligned}$$

where $k = 3, 1, 0$ respectively for option (A), (B), (C).

Now we have specified all our parameters and we shall calculate the eigenvalue λ_0 with the aid of a numerical procedure. The results are summarized in table 6.

Female breeding population F	50000	70000	90000
survival rate s after corrections for decreasing initial year classes and hunt	0.931	0.894	0.874
λ_0 - value without hunt, option (A)	1.112	1.082	1.065
λ_0 - value without hunt, option (B)	1.134	1.094	1.072

Table 6. Calculation of eigenvalue λ_0 without hunt
(r_i - values from table 2)

We perform the same calculations with the parameters given by Jacobsen (1979): table 3 and five choices for the instantaneous natural mortality: $i = 0.08, 0.10, 0.12, 0.14, 0.16$, where $i = -\ln(s)$. See table 7.

Instantaneous natural mortality i	Natural survival rate $s = \exp(-i)$	λ_0 - value without hunt, option (C)
0.08	0.923	1.128
0.10	0.905	1.105
0.12	0.887	1.084
0.14	0.869	1.062
0.16	0.852	1.041

Table 7. Calculation of eigenvalue λ_0 without hunt
(r_i - values from table 3)

4.6. Age distribution with hunt

All these calculations correspond to an unhunted population, because we used the natural survival rates. Next we will consider the effect of the hunt on the population. It is possible to do this in two ways. Namely firstly to use the survival rate computed from the sample and corrected for the decreasing initial year classes, but not corrected for the hunting influences. The corresponding calculations are summarized in table 8.

Female breeding population F	50000	70000	90000
survival rate s after correction for decreasing initial year classes	<hr/>		
λ_0 - value with hunt, option (A)		0.811	
λ_0 - value with hunt, option (B)		1.014	
		1.003	

Table 8. Calculation of eigenvalue λ_0 with hunt
(r_i - values from table 2)

To be able to evaluate the influences of a certain hunting pressure to the population, absolute values or estimates concerning the population size are necessary as the hunting statistics are absolute. The absolute catch of each year class has to be expressed as a fraction of the absolute year class size in the population. After the hunt the absolute numbers

x_i^{N+1} can be expressed in terms of the numbers x_i^N , the coefficients r_n , s_n and the catch numbers $C_{n,N+1}$. We split the number $C_{11,N+1}$ in the following way. Define

$C'_{11,N+1}$ = catch, number of animals aged 11, caught in year $N+1$.

$C''_{11,N+1}$ = catch, number of animals aged ≥ 12 , caught in year $N+1$.

By this definition we have $C_{11,N+1} = C'_{11,N+1} + C''_{11,N+1}$. The evolution of the population from year N to year $N+1$ can then be written as (option (A))

$$x_0^{N+1} = \frac{1}{2} r_3 s_0 x_2^N + \frac{1}{2} \sum_{i=3}^{11} r_{i+1} s x_i^N - C_{0,N+1} \quad (r_{12} = r_{11}),$$

$$x_i^{N+1} = s_0 x_{i-1}^N, \quad i = 1, 2, 3,$$

$$x_i^{N+1} = s x_{i-1}^N - C_{i,N+1}, \quad i = 4, \dots, 10,$$

$$x_{11}^{N+1} = s x_{10}^N + s x_{11}^N - C_{11,N+1},$$

With obvious changes for options (B) and (C). Furthermore we take

$C_{1,N+1} = C_{2,N+1} = C_{3,N+1} = 0$ as these immature individuals are rarely seen in the breeding area and therefore are scarcely or not at all represented in the breeding population catch sample. Let us introduce some numbers:

K = total number of female animals aged ≥ 4 .

Q = total number of killed female animals aged ≥ 4 .

$b_i = C_{i,N+1} / Q$, $i = 4, \dots, 10$,

$b'_{11} = C'_{11,N+1} / Q$,

$b''_{11} = C''_{11,N+1} / Q$.

By this definition we have $\sum_{i=4}^{10} b_i + b'_{11} + b''_{11} = 1$, and

$$C_{i,N+1} = b_i Q = b_i (Q/K) (K/x_{i-1}^N) x_{i-1}^N, \quad i = 4, \dots, 10,$$

$$C_{11,N+1} = (b'_{11} + b''_{11}) Q = b'_{11} (Q/K) (K/x_{10}^N) x_{10}^N + \\ b''_{11} (Q/K) (K/x_{11}^N) x_{11}^N.$$

We can estimate the numbers b_i , $i = 4, \dots, 10$, b'_{11} and b''_{11} from the catch sample. In first approximation the expression K/x_i^N can be approximated by the knowledge of the age distribution for the unhunted population and finally the quotient Q/K can be estimated by the hunting statistics and an estimate for the total female population. The numbers b_i have been calculated from the 1975 sample, see tables 1 & 9. For the calculation of K/x_i^N we used the eigenvector $\underline{\hat{x}}^N$. Then we find the following (option (A)) expressions:

$$K = \sum_{i=4}^{i=10} \lambda^{-i} (s_0)^3 (s)^{i-3} + \lambda^{-10} (\lambda-s)^{-1} (s_0)^3 (s)^8 =$$

$$\lambda^{-3} (\lambda-s)^{-1} (s_0)^3 s,$$

$$K/x_i^N = \lambda^{i-3} (\lambda-s)^{-1} (s)^{4-i}, \quad i = 4, \dots, 10,$$

$$K/x_{11}^N = \lambda^7 (s)^{-7},$$

again with obvious changes for options (B) and (C). According the definition Q is known from the hunting statistics; we take $Q = 6500$.

Define: X = total number of female pups produced by females aged ≥ 4 . The relation between X and K can be expressed as

$$K = 2 \left(\sum_{i=4}^{i=11} b_i / r_i \right) X,$$

because, if we suppose that the catch sample reflects the frequency of female year classes, there will be $b_i X$ female pups produced by females aged i . Then there will be present in this year class $2(b_i / r_i) X$ females, in view of the age specific reproduction rate. By sommation we find the expression for K . In table 9 we have done the corresponding calculations.

age i	4	5	6	7	8	9	10	11	≥ 12	Σ
# $\frac{00}{11}$	15	25	39	41	31	17	17	12	62	259
b_i	0.0579	0.0965	0.1506	0.1583	0.1197	0.0656	0.0656	0.0463	0.2394	1
* r_i	0.556	0.716	0.826	0.935	0.944	0.944	0.960	0.980	0.980	
* b_i/r_i	0.104	0.135	0.182	0.169	0.127	0.070	0.068	0.047	0.244	1.146
** r_i	0.390	0.713	0.912	0.950	0.950	0.950	0.950	0.950	0.950	
** b_i/r_i	0.149	0.135	0.165	0.167	0.126	0.069	0.069	0.049	0.252	1.181

Table 9. Calculations of the numbers b_i and b_i/r_i
 (* according table 2; ** according table 3)

In table 10 we have calculated $t = Q/K$ for the three different hypotheses for the total number of female pups produced by females aged ≥ 4 (i.e. X).

Finally we have to make a correction for the hunt of the pups. This can be done by lowering the age specific reproduction rate by a factor $(1-t_1)$, where

$$t_1 = Y/X, \text{ with}$$

Y = total number of caught female pups.

From the hunting statistics an estimate for Y is $Y = 10000$ (Øritsland & Benjaminsen (1975a)). See table 10. The allowed quota for 1977 was 33500, for 1981 20000 male and female pups together.

After all these adjustments we can put the evolution from year N to $N+1$ again in a matrix form, where the coefficients have been changed. The survival rates are however now depending on the value λ_0 belonging to the unhunted population. To solve this, we calculate the new value λ_0' and the corresponding eigenvector, which we use for a new estimate of K/x_i^N . It means that we modify our survival rates. Then we calculate the eigenvalue: λ_0'' .

Born female pups $X = \frac{1}{2} F$	25000	35000	45000
$t_1 = Y/X_1$ where $Y = 10000$	0.400	0.286	0.222
caught females Q	6500	6500	6500
* total number females aged $\geq 4 : K = 2 (1.146) X$	57300	80220	103140
$t = Q/K$	0.113	0.081	0.063
** total number females aged $\geq 4 : K = 2 (1.181) X$	59050	82670	106290
$t = Q/K$	0.110	0.079	0.061

Table 10. Calculation of the numbers t and t_1
 (* according table 2; ** according table 3)

We repeat this procedure until the new found eigenvalue differs not more than 5_{10}^{-6} from the old one. In practice we had to do at most 7 iterations. In this way we have solved a nonlinear eigenvalue problem. We remark that after the first iteration the eigenvector does not possess the simple form as we have exhibited, but still it can be calculated. In table 11 the results are given for the options (A) and (B) and the r_i -values from table 2. In table 12 the results are given for option (C) and the r_i -values from table 3. Jacobsen (1979) points out that the value $s = \exp(-0.12)$ and a total production of 50000 pups is the most reliable.

Female breeding population F	50000	70000	90000
t - value	0.113	0.081	0.063
t_1 - value	0.400	0.286	0.222
λ_0 - value with hunt, option (A)	0.989	0.999	1.001
λ_0 - value with hunt, option (B)	1.009	1.008	1.007

Table 11. λ_0 - value with hunt, calculated with iteration
 procedure (r_i - values from table 2)

Female breeding population F	50000	70000	90000
t - value	0.110	0.079	0.061
t_1 - value	0.400	0.286	0.222
λ_0 - value with hunt, option (C),			
for $s = \exp(-0.08) = 0.923$	1.006	1.043	1.063
$s = \exp(-0.10) = 0.905$	0.985	1.021	1.041
$s = \exp(-0.12) = 0.887$	0.964	1.000	1.020
$s = \exp(-0.14) = 0.869$	0.944	0.980	0.999
$s = \exp(-0.16) = 0.852$	0.924	0.959	0.979

Table 12. λ_0 - value with hunt, calculated with iteration procedure (r_i - values from table 3)

5. DISCUSSION

If we take the results of Jacobsen (1979) for granted, i.e. $s = \exp(-0.12)$, the r_i - values from table 3 and the estimate of the production of 50000 pups, then the results of table 12 indicate that the quota until 1975 which resulted in averaged 6500 adult females annually killed, was too high, because the found λ_0 - value (0.964) is less than 1. Since that time the hunting pressure on the adult females has been lowered. In 1981 the quota was "none or maximal 2% of pups", it means a maximum of 400 adult females.

Besides, the results of tables 11 and 12 give the impression that the hunting pressure is just equal or more than the population can stand, while Jacobsen (1979) points out that there is still uncertainty in the production estimate of 50000 pups and in the instantaneous natural mortality value (0.12). It seems that it has not been tried to estimate the breeding population by an independent method (e.g. aerial survey). This information should resolve a lot of uncertainty. If it should turn out that the population is substantially smaller than 59000 adult females (4-year and older) - see table 10 (59050), which fits with the projection of Jacobsen (1979) for 1979 (pup production 50000, 4- year and older females 59419) - then the quota is still

too high. The catch results of the last seasons (1976-1980) have been much lower than the quota, which partly is caused by less effort of the norwegian sealers (fewer ships), partly by the ice-conditions. But it might be also reflect a much worsened situation of the population as a whole. A very restrictive policy as long as the population dynamics are not fully understood seems appropriate.

Acknowledgement

By life the first author enjoyed the hospitality and the support of the Institute for Taxonomic Zoology, University of Amsterdam, where he performed the analysis of the lower canines. Financial support was given by grants of the "Van Tienhoven Stichting" and the Netherlands Foundation for Arctic Biological Research.

The authors thank T. Aldenberg for valuable advise concerning the literature.

REFERENCES

- CHAPMAN, D.G., & D.S. ROBSON, (1969), *The analysis of a catch curve*, Biometrics 16, 354-369.
- HEINCKE, F., (1913), *Investigations on the plaice. General Report. I. The plaice fishery and protective measures. Preliminary brief summary of the most important points of the report*, Cons. Intern. Explor. Mer., Rapp. et Proc.-Verb. 16, 1-67.
- JACOBSEN, N.O., (1979), *Produksjon, alder ved første gangs kasting og naturlig dødelighet hos klappmyss, Cystophora cristata* (Erxleben, 1777), i *Vesterisen*, Institutt for fiskeribiologi: Unversitetet i Bergen.
- LAWS, D., (1976), *Age determination of pinnipeds with special reference to growth layers in teeth*, Z. Säugetierk. 27, 129-146.
- LESLIE, P.H., (1945), *On the use of matrices in certain population mathematics*, Biometrika 33, 183-212.

- PIELOU, E.C., (1969), *An Introduction to Mathematical Ecology*, New York, Wiley-Interscience.
- ROBSON, D.S., & D.G. CHAPMAN, (1961), *Catch curves and mortality rates*, Trans. Am. Fish. Soc. 91, 181-189.
- SERGEANT, D.E., (1976), *History and present status of populations of Harp and Hooded Seals*, Biol. Conserv. 10, 95-118.
- ØRITSLAND, T., (1975), *Sexual maturity and reproductive performance of female hooded seals at Newfoundland*, Int. Comm. Northw. Atl. Fish. Res. Bull. 11, 37-41.
- ØRITSLAND, T., & T. BENJAMINSEN, (1975a), *Rapport om Norske selundersøkelser og Norsk selfangst i det Nordøstlige Atlanterhav i 1975*, Notat Fiskeridir. Havforskn. Inst. dec. 1975, 1-30. Mimeographed.
- ØRITSLAND, T. & T. BENJAMINSEN, (1975b), *Sex ratio, age composition and mortality of hooded seals at Newfoundland*, Int. Comm. Northw. Atl. Fish. Res. Bull. 11, 135-143.

