Estimating the survival rate of Northern fur seals (Callorhinus ursinus) on different stage of its lifecycle based on long-term observations of Tyuleniy herd

Modeling the population number dynamics

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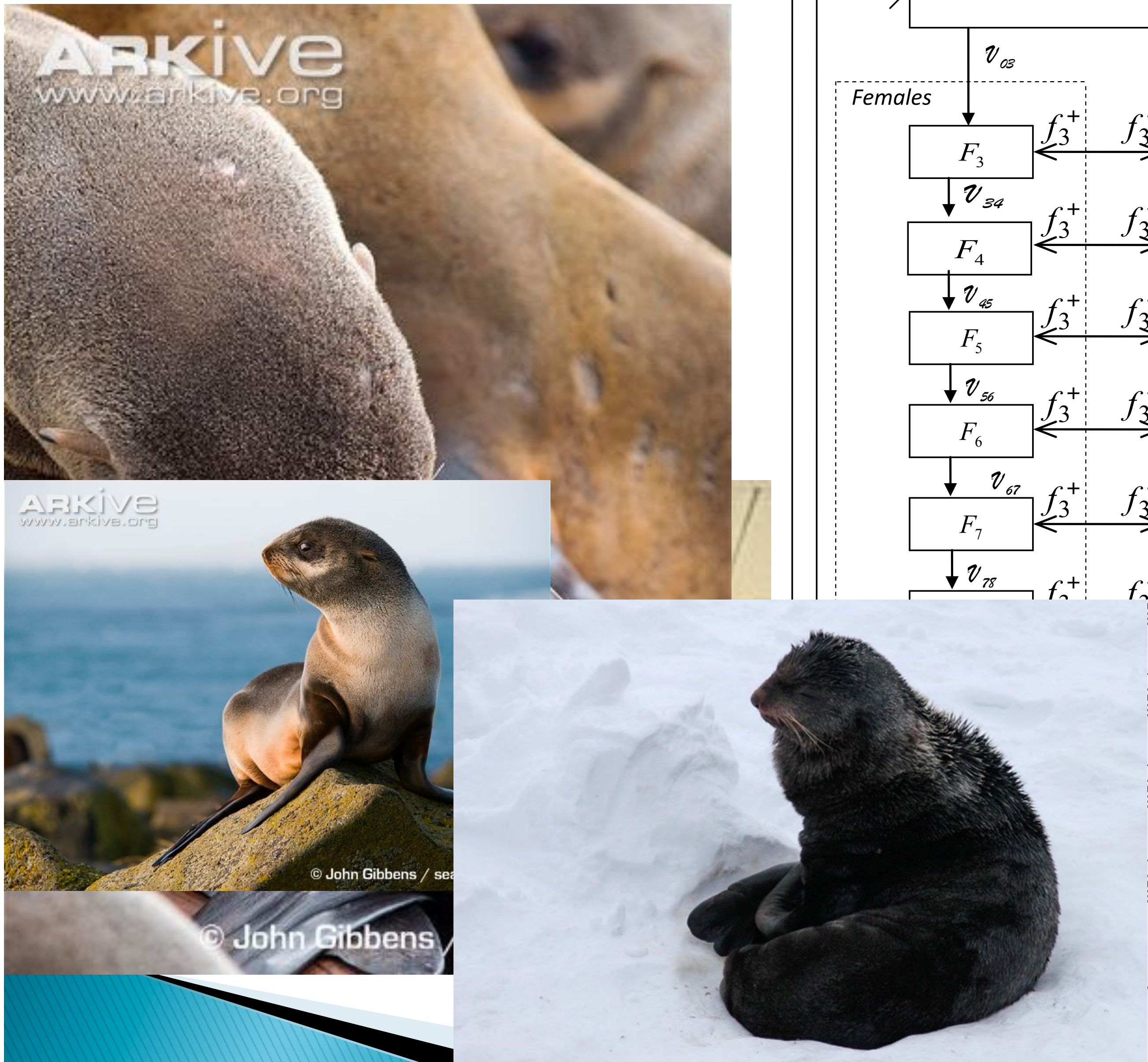
History

- In the middle of the last century the northern fur seal became the attractive object for population investigations.
- During 30-years period of existence of the Interim Convention of Conservation of North Pacific Fur Seals a unique set of data on the population dynamics of this species has been accumulated and it became a good base for estimating population parameters and developing various mathematical models of population dynamics.
  - Interim Convention on Conservation of North Pacific Fur Seals: http://sedac.ciesin.columbia.edu/entri/texts/acrc/fur.seals.1957.html

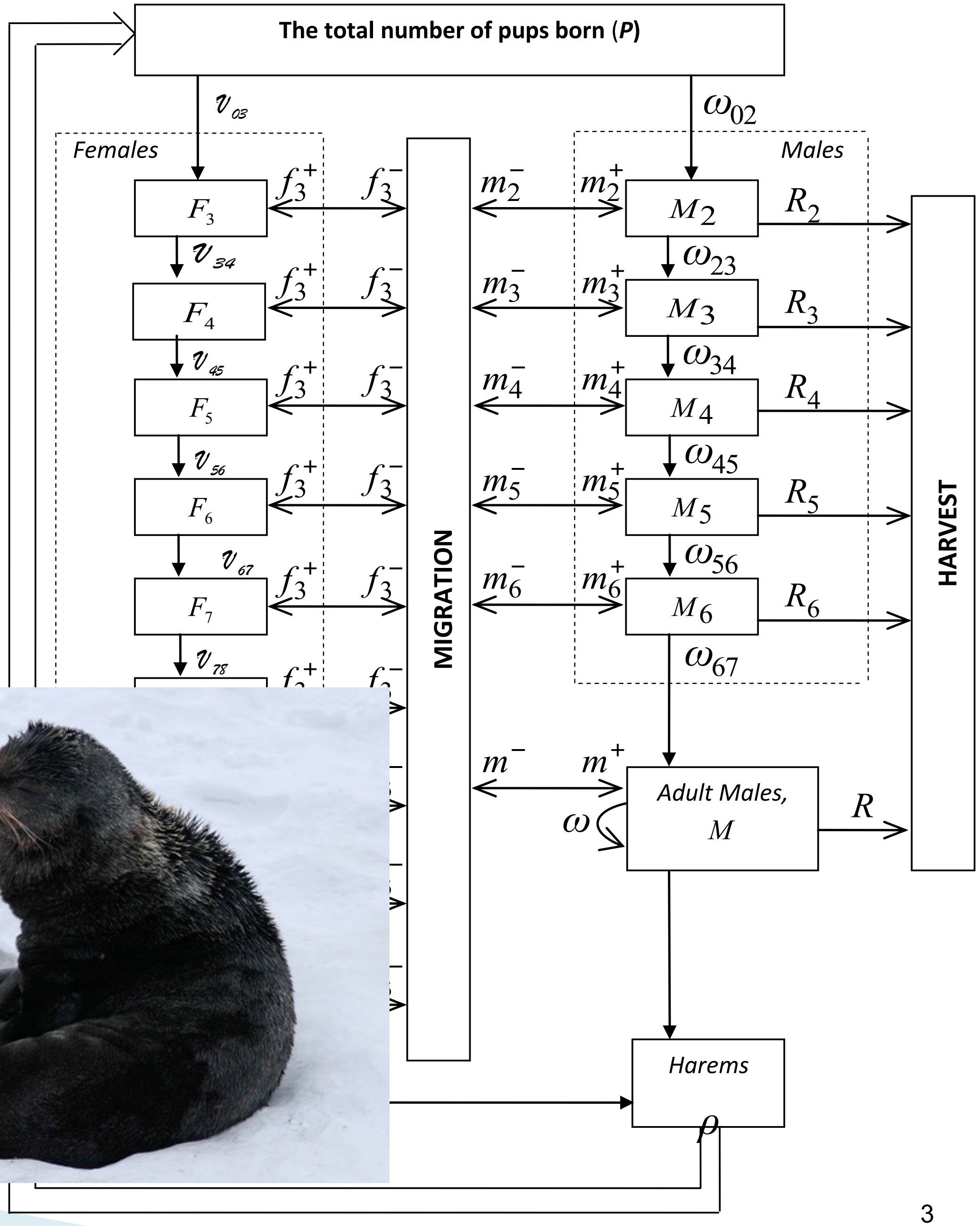
- In particular, the detailed model of fur seals dynamics and techniques of calculating its parameters were developed.
  - E.Ya. Frisman, E.I. Skaletskaya, A.E. Kuzyn. (1982) A mathematical model of the population dynamics of a local northern fur seal with seal herd, Ecol. Mod., 16: 151-172.

- By now significantly increased data series allow us to verify the suitability of the constructed model and the techniques of calculating the intrapopulation parameters, taking into account possible changes in intrapopulation and harvesting processes.
  - R.H. Lander. (1975) Method of determining natural mortality in the northern fur seal (Callorhinus ursinus) from known pups and kill by age and sex, J. Fish. Res. Board Can., 32(12): 2447-2452.
  - A.W. Trites. (1989) Estimating the juvenile survival rate of male northern fur seals (Callorhinus ursinus), Can. J. Fish. Aquat. Sci., (46): 1428-1436.

- **Birth process** – Birth process – northing fur seal pups born
  - λ



Flow-chart for the lifecycle of fur seal



A mathematical model of the local population dynamics

F_0 and M_0 – the number of male and female pups accordingly;
$F_0 = M_0 = P/2$
F – the number of adult females, $F = \Sigma F_i$, $i \geq 3$

$$2F_0(n) = 2M_0(n) = P(N) = \lambda F(n); \qquad (1)$$

$$F_3(n) = v_{03}(n-3)F_0(n-3); \qquad (2)$$

$$F_{i+1}(n) = v_{i,i+1}(n-1)F_i(n-1), \;\; i = \overline{3,9}; \qquad (3)$$

$$F_{11}(n) = v_{10,11}(n-1)F_{10}(n-1) + v(n-1)F_{11}(n-1); \qquad (4)$$

$$M_2(n) = w_{02}(n-2)M_0(n-2); \qquad (5)$$

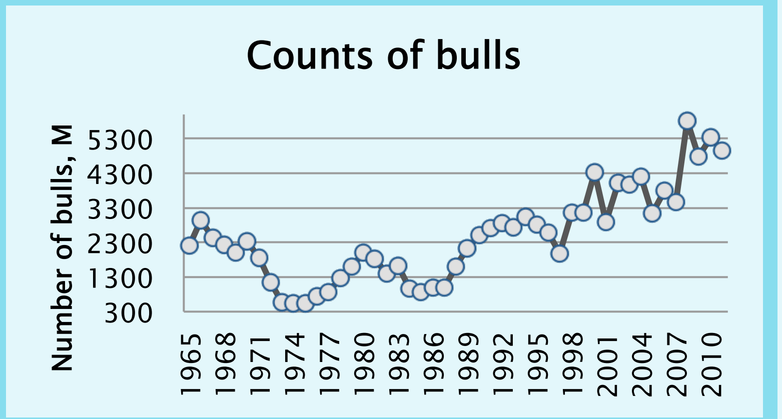
$$M_{i+1}(n) = w_{i,i+1}(n-1)(M_i(n-1) - R_i(n-1)), \;\; i = \overline{2,5}; \qquad (6)$$

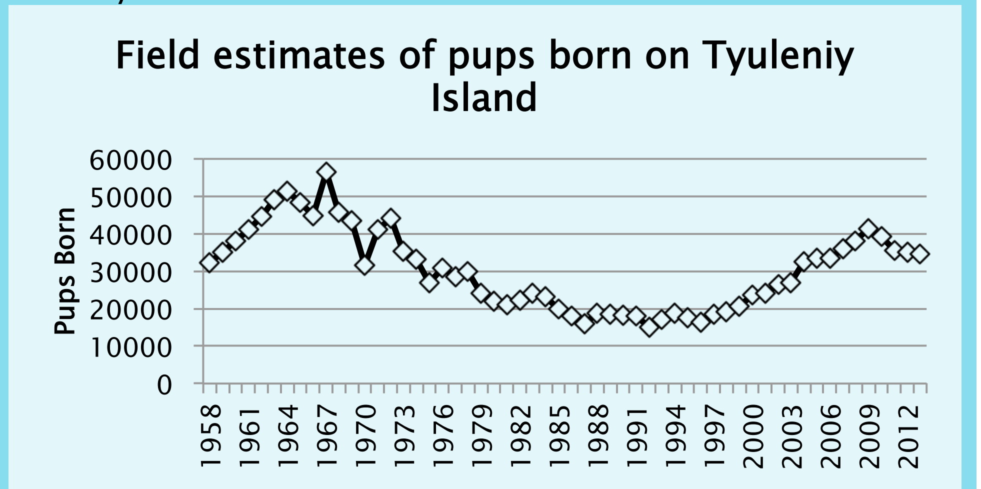
$$M(n) = w_{6,7}(M_6(n-1) - R_6(n-1)) + w(n-1)(M(n-1) - R(n-1)), \qquad (7)$$

- λ – pregnancy rate,
- $v_{i,j}$ and $w_{i,j}$ – survival rates from age i to j years for females and males accordingly,
- v – survival rate of females 11 years old and older,
- w – survival rate of harem bulls,
- R_i – the number of males killed in age of i–years (i=2,…,6),
- R – the number of males killed in age after 6 years.

Questions and problems

- <u>The main question:</u> What does occur in Tyuleniy herd of northern fur seals?
  - During a lot of years of harvesting this population (the strategy of hunting proposed to be optimal), its number had reduced and the population fell in long depression. – *The problem like this is noted for other populations of Northern Pacific: Commander and Pribilof fur seals*.
  - To conserve the population the hunting was reduced considerably and after 2008th yr. exploitation of this herd was interrupted at all. It results in considerable growth of bulls number, but pups born (despite a slight increase) does not reach the values of the middle of 60^{th} yr.





<u>The present work</u>

Problems:

- 1. Estimating the model parameters: dynamics of survival rates of males and females on various stages of lifecycle
  - The Cause of slow and uncertain population growth may be due to a sharp reduce in survival rates of juveniles or other age groups
- 2. Correcting the general model
  - Testing the existence of a density dependence effects in juvenile survivals
  - Influence of sexual ratio in the population on females' pregnancy rates
  - Understanding the evolutionary consequences of the harvest: was it really unselective one, that did not force the bulls to grow weak?

3. Constructing the more accurate the forecast and the management strategy

The data (1 from 2)

- The harem bull counts (1958 – 2013 yr.)
- The total number of pups born (1958 – 2013 yr.)
- The number and age composition of males taken in the commercial harvest (1958 – 2008 yr.)
    - The selective congregation of immature fur seals makes it possible to drive and kill primarily the valuable 3- and 4-yr olds without interfering with the breeding animals
- The age composition of the male component of the herd is unknown

- The number and age compositions of the female component of the herd is unknown

- The lower estimate of adult females number is total number of pups born

$$F_L(n) = P(n)$$

- Data from marine samples: females were investigated biologically
  - For each female from marine sample there are data about her age and pregnancy
  - (1958-1988 yr.)

Estimating the juvenile survival of males (from birth to 2 yr)

Lander procedure and its modifications

- The Lander's assumption about harvest strategy (II) is violated for males born in yr: 1962, 1981, 1983, 1991, 1992, 2003 and 2004;
  - Here $R_{4+}(n) > R_4(n)$
  - Years without harvest :1987, 1995, 1996, 2007 and after 2008.
- The modification (Frisman et al., 1982)
  - II*. $R_3(n) \geq M_3(n)/2$
- New modification for males born in 1992 yr.
  - II**. $M_{5U}=R_2+R_5$

The main assumptions of Lander procedure

I. Subadult survival (from 2 to 5 yr of age) is constant
   - $w_{45}(n\text{-}1) = w_{34}(n\text{-}2) = w_{23}(n\text{-}3) = w_{25}(n\text{-}3)$;

II. About harvest strategy – the exploitation of 4-yr olds exceeded 50%
   - $(R_4(n) \geq M_4(n)/2)$.

Formulas for calculation

$$w_{02L}(n-5) = \frac{R_2(n-3)}{M_0(n-5)} + \frac{R_3(n-2)}{M_0(n-5)} w_{25}^{-1} + \frac{R_4(n-1)}{M_0(n-5)} w_{25}^{-2} + \frac{R_5(n)}{M_0(n-5)} w_{25}^{-3}$$

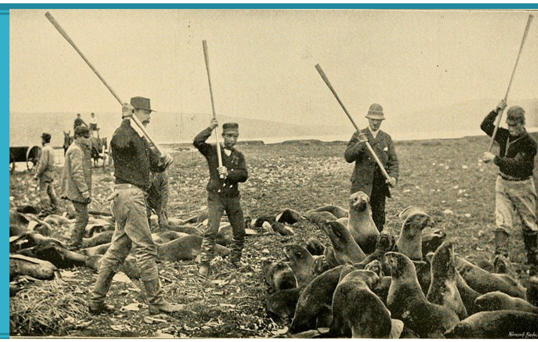
$$w_{02U}(n-5) = \frac{R_2(n-3)}{M_0(n-5)} + \frac{R_3(n-2)}{M_0(n-5)} w_{25}^{-1} + \frac{R_4(n-1)}{M_0(n-5)} w_{25}^{-2} + \frac{R_5(n)+R_4(n-1)}{M_0(n-5)} w_{25}^{-3}$$

Determining the w_{25L} by numerical solving following:

$$\mu_{02L} = (-\ln w_{02U})/24 \geq \mu_{25} = (-\ln w_{25})/11$$

and then

$$w_{25} = \frac{R_4 + (R_4+R_5)(1+w_{25L}^{-1})}{(R_4+R_5)(1+w_{25L}^{-2}) + R_4 w_{25L}^{-1}} \qquad w_{02} = \frac{1}{2}(w_{02L} + w_{02U})$$

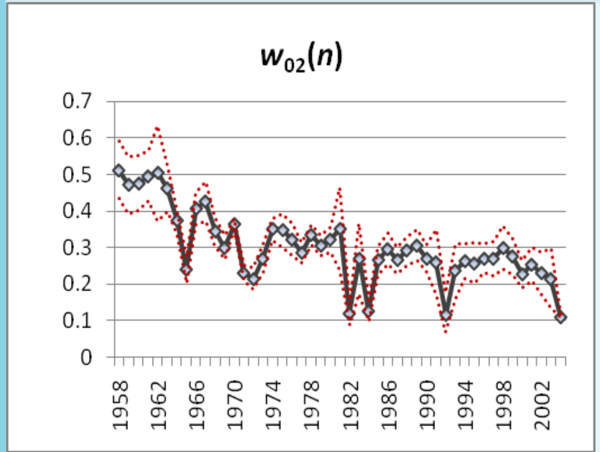


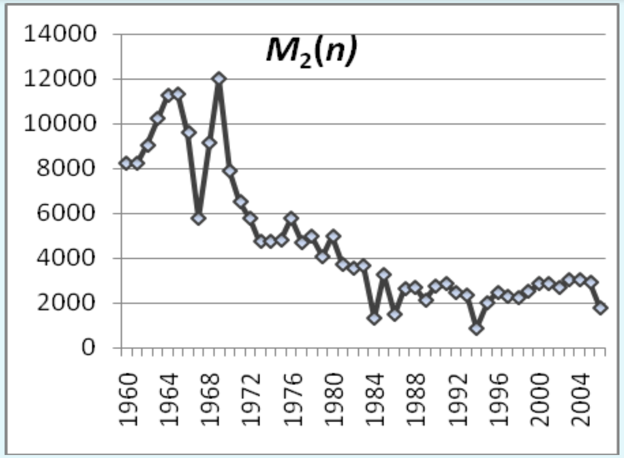
Results: Estimating the juvenile survival of males (from birth to 2 yr) *Lander procedure and its modifications* and next calculations

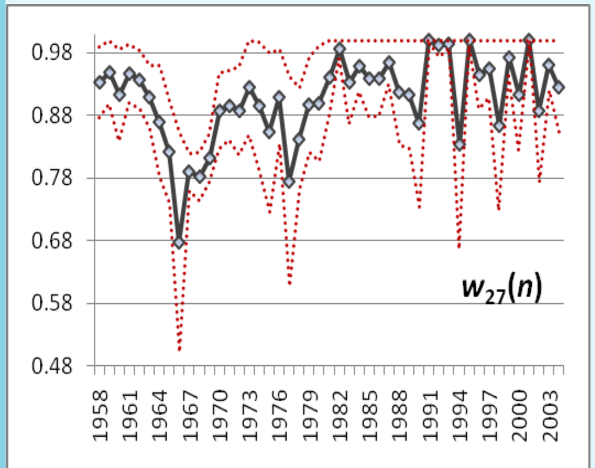
- The number of 2-yr olds: $M_2(n+2)=M_0(n)w_{02}(n)$
- The survival rate of subadults (from 2 to 7 yr) w_{27} – by procedure (Frisman et. al., 1982): $M_7 = (((((M_2 - R_2)w_{27} - R_3)w_{27} - R_4)w_{27} - R_5)w_{27} - R_6)w_{27}$
  - M_7 - ???
  - $w_{27} = w_{27U}$: $M(n) \geq M_7(n)$
  - $w_U = w_{27L}$:

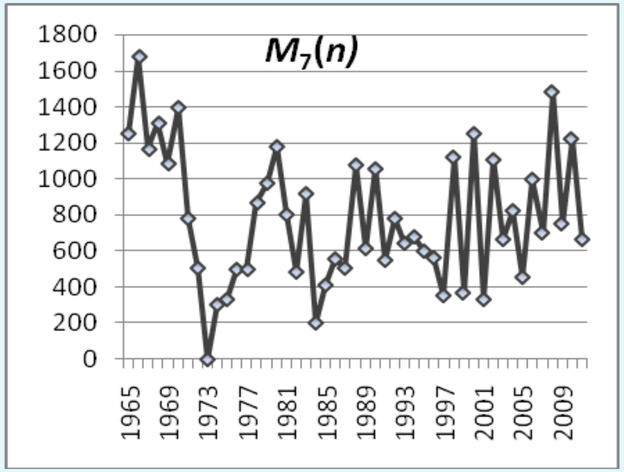
$$M(n) - (M(n\text{-}1) - R(n\text{-}1))w_{27L} = (((((M_2(n\text{-}5) - R_2(n\text{-}5))w_{27L} - R_3(n\text{-}4))w_{27L} - R_4(n\text{-}3))w_{27L} - R_5(n\text{-}2))w_{27L} - R_6(n\text{-}1))w_{27L},$$

  - then: $w_{27} = (w_{27U} + w_{27L})/2$.





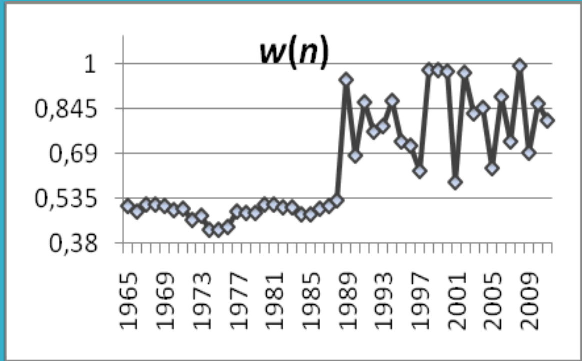


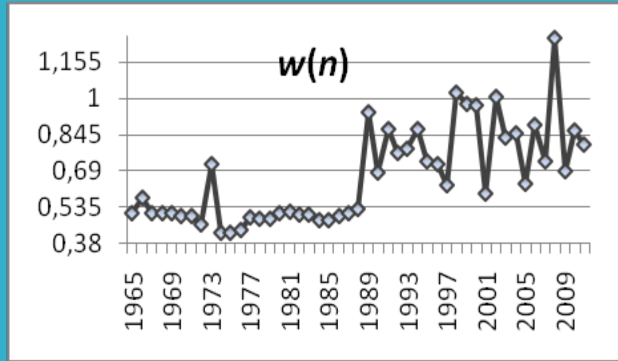


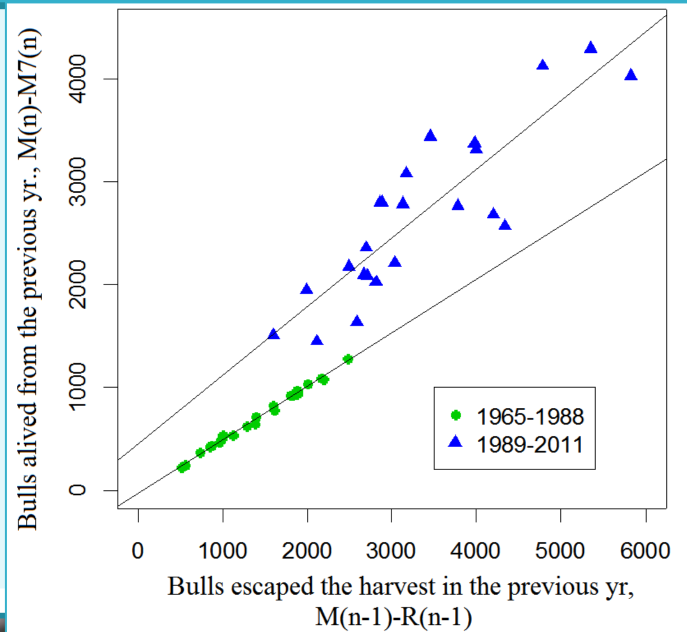
- The proportion of bulls surviving from one year to the next is $w(n)$: $w(n) = (M(n) - M_7(n))/(M(n\text{-}1) - R(n\text{-}1))$

- The data set is inhomogeneous
  - There are two periods: 1965 – 1988yr. and 1989 – 2011yr.

- Linear regression:
- $M(n)$ - $M_7(n) = w(M(n\text{-}1)\text{-}R(n\text{-}1))$
  - Each time interval (before 1988 yr and after) is treated separately
  - Outliers corrections (M_7): 1966, 1973, 2008;
  - Correction of M_7, that give $w(n)$>1: 1998, 2002 and 2008 yr.







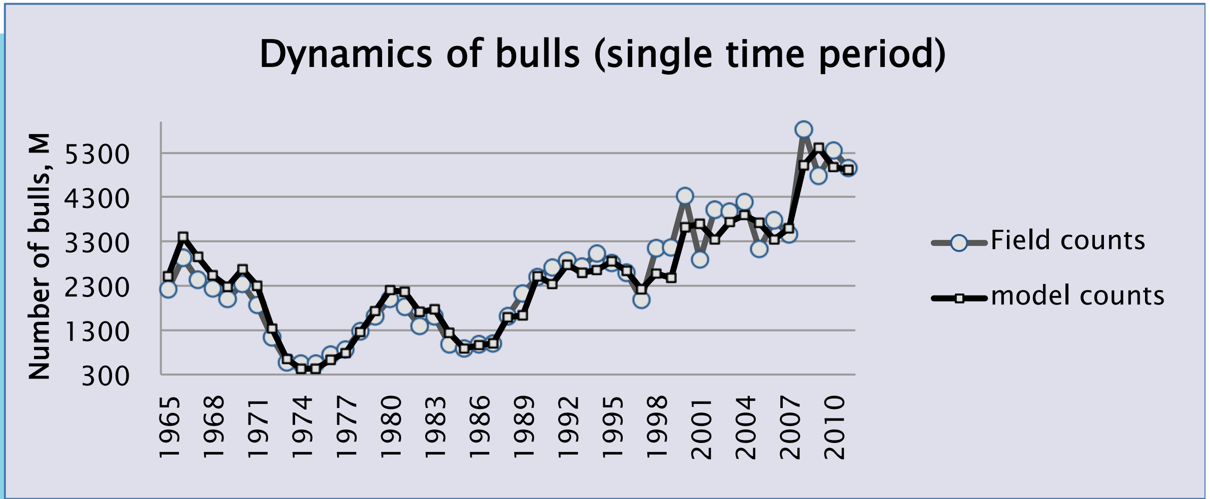
- The model:

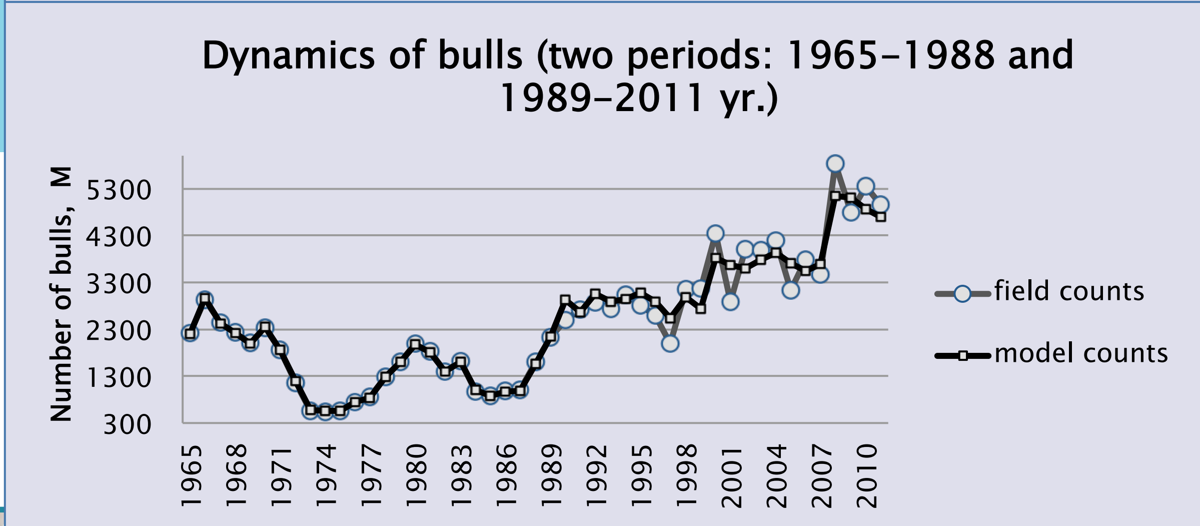
$$M_2(n) = w_{02}(n-2)M_0(n-2);$$

$$M_7(n+5) = (((((M_2(n) - R_2(n))w_{27}(n) - R_3(n+1))w_{27}(n) - R_4(n+2))w_{27}(n) - R_5(n+3))w_{27}(n) - R_6(n+4))w_{27}(n)$$

$$M(n+5) = M_7(n+5) + w(M(n+4) - R(n+4)).$$

The observations of pups number ($P/2=M_0$), harvest (R_i), and rates calculated (w_{02}, w_{27} and w) are utilized in the model.



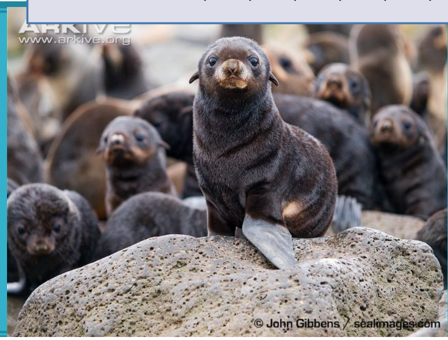


<u>For single time interval the mean error of approximation is</u>

A=12.2%

<u>For two time intervals and with M_7 correction</u>

A=5.5%.



Results and issues

- In large mammal populations juvenile survival is
  - a key component of population dynamics,
  - a potential indicator of population status

- It seems that Lander method and it modifications give **inaccurate estimates** for this parameter (juvenile survival of males, w_{02}).
  - To obtain an adequate dynamics of male component of herd we have to correct:
    - a bias in calculated values of M_7
    - outliers - This is especially evident for the later period (1989 – 2011 yr), which may be due to a sharp change in the nature of the harvest strategy .
- Accuracy of Lander procedure depends considerably on assumption of 50% utilization in harvest
  - it based on Lander's insight into the harvest rather than on data;
  - underestimating the values of w_{02} results in regular upward bias of survival rates for next ages w_{27} and w.
- It is necessary to develop new procedures for calculating the more correct estimates of juvenile survival of males

Estimating the juvenile survival of males (from birth to 2 yr) (*Other methods)*

- There are three modifications in (Trites A.W., 1989. Estimating the juvenile survival rate of male northern fur seals (*Callorhinus ursinus*) // Canadian Journal of Fisheries and Aquatic Sciences. V. 46. P. 1428–1436.) based on Chapman (1964) and Smith-Polacheck (1984) methods.
  - All these methods use assumption about harvest strategy too

$$(a)\; w_{02L} = \frac{R_2 + R_3 w_{27}^{-1} + R_4 w_{27}^{-2} + R_5 w_{27}^{-3} + R_6 w_{27}^{-4}}{M_0}$$

$$(b)\; w_{02U} = \frac{R_2 + R_3 w_{27}^{-1} + 2R_4 w_{27}^{-2}}{M_0}$$

- (a) $w_{27} \rightarrow w_{27U} = 1$
- (b) $w_{27} \rightarrow w_{27\mathrm{L}} = (w_{02})^{0.5}$
- the upper estimate calculation is based on the assumption,

that at least 50% of the 4-yr old males were killed under management policies

Formulas for calculation without any assumption about harvest strategy :

$$w_{02} = (w_{02L} + w_{02U})/2$$

$$(a)\; w_{02L} = \frac{R_2 + R_3 w_{27}^{-1} + R_4 w_{27}^{-2} + R_5 w_{27}^{-3} + R_6 w_{27}^{-4} + M_{7L} w_{27}^{-5}}{M_0}$$

$$(b)\; w_{02U} = \frac{R_2 + R_3 w_{27}^{-1} + R_4 w_{27}^{-2} + R_5 w_{27}^{-3} + R_6 w_{27}^{-4} + M_{7U}(n) w_{27}^{-5}}{M_0}$$

$$M_{7L}(n) = M(n) - w_{27}(M(n-1) - R(n-1))$$

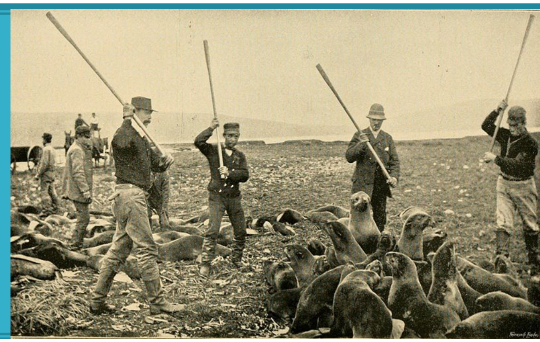
$$M_{7U}(n) = M(n)$$

(w_{02L}) : $w_U = w_{27U} = 1$

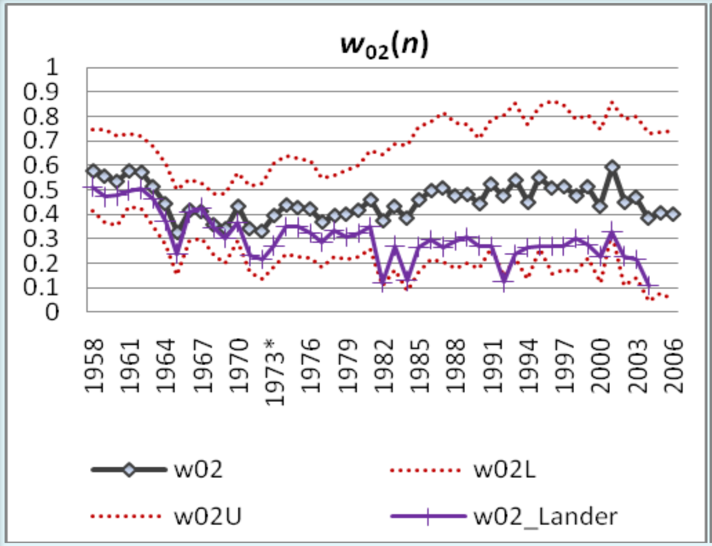
$$\boxed{w_{02L} = \frac{R_2 + R_3 + R_4 + R_5 + R_6 + M_{7L}}{M_0} \qquad M_{7L}(n) = M(n) - (M(n-1) - R(n-1))}$$

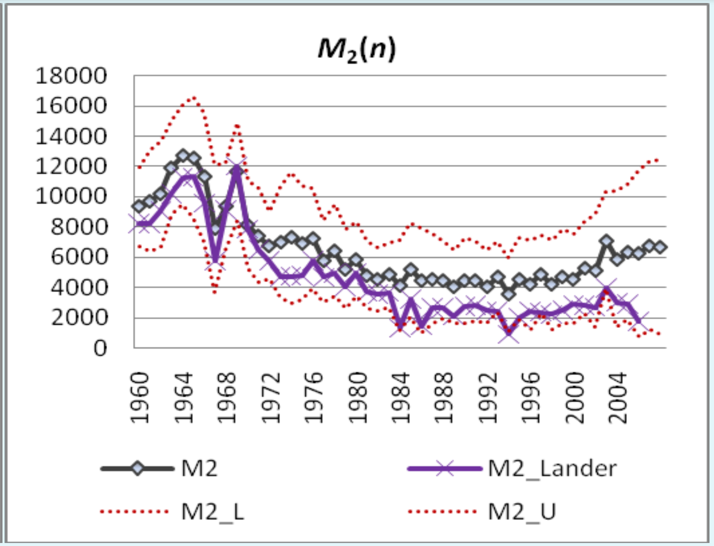
(w_{02U}): $(w_{27L} = (w_{02U})^{0.5}$, $w = 0)$

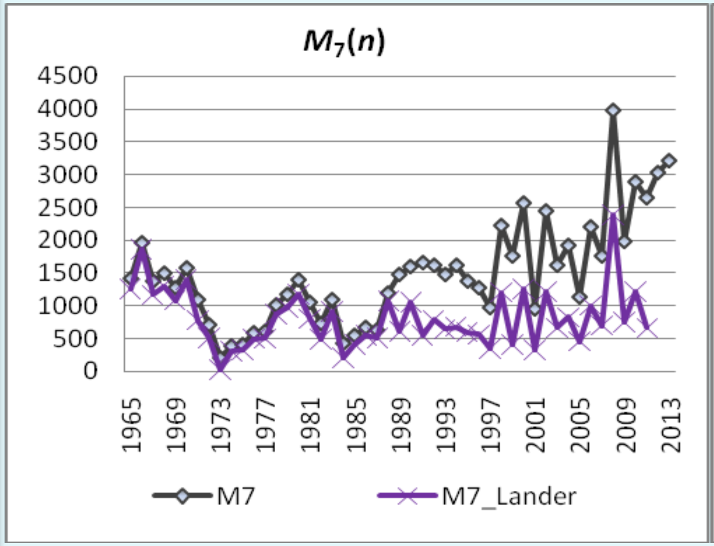
$$\boxed{w_{02U} = \frac{R_2 + R_3((w_{02U})^{-0.5} + R_4(w_{02U})^{-1} + R_5(w_{02U})^{-1.5} + R_6(w_{02U})^{-2} + M_{7U}(n)(w_{02U})^{-2.5}}{M_0} \qquad M_{7U}(n) = M(n)}$$

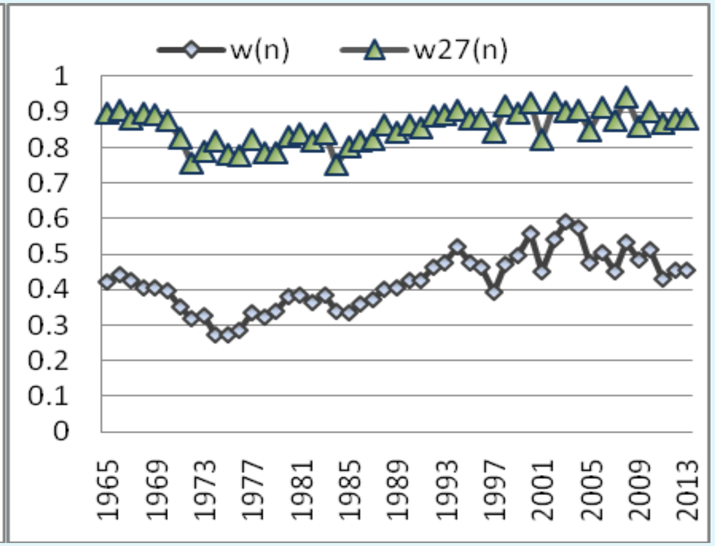


Results: Estimating the juvenile survival of males (from birth to 2 yr) *the new method* and next calculations (1 from 2)









Results: Estimating the juvenile survival of males (from birth to 2 yr) *the new method* and next calculations (2 from 2)

- 1965-1988 yr:

$M(n) - M_7(n) = 0.446 \cdot (M(n-1)-R(n-1)) - 99.2$

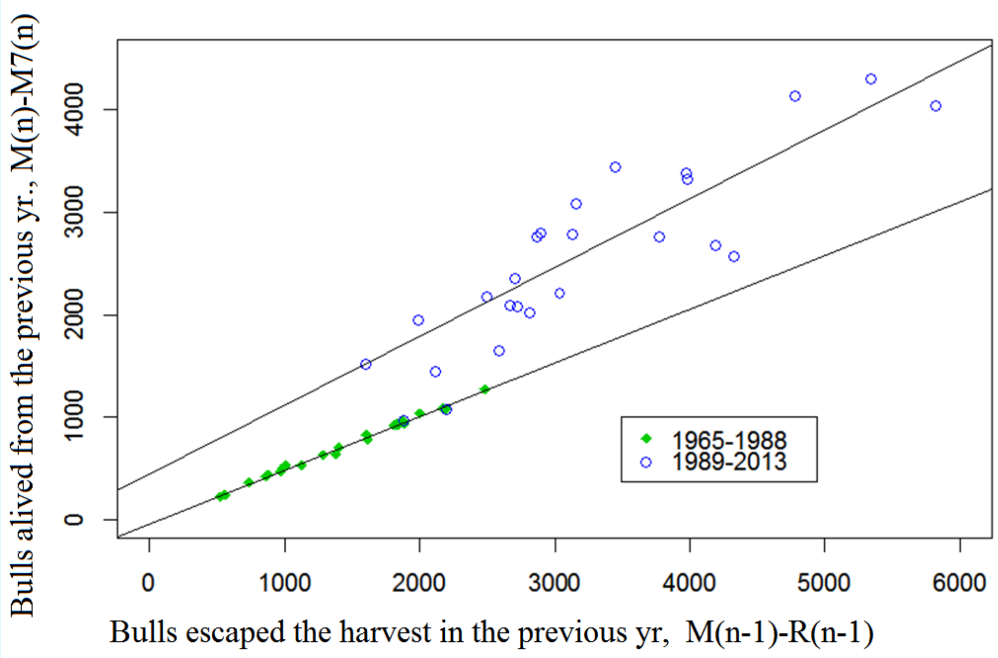
  - R^2=0.97,
  - Both regression coefficients are significant on $\alpha = 0.01$ level
  - i.e. the number of a seven-year old males is overestimated on 99 individuals in average.

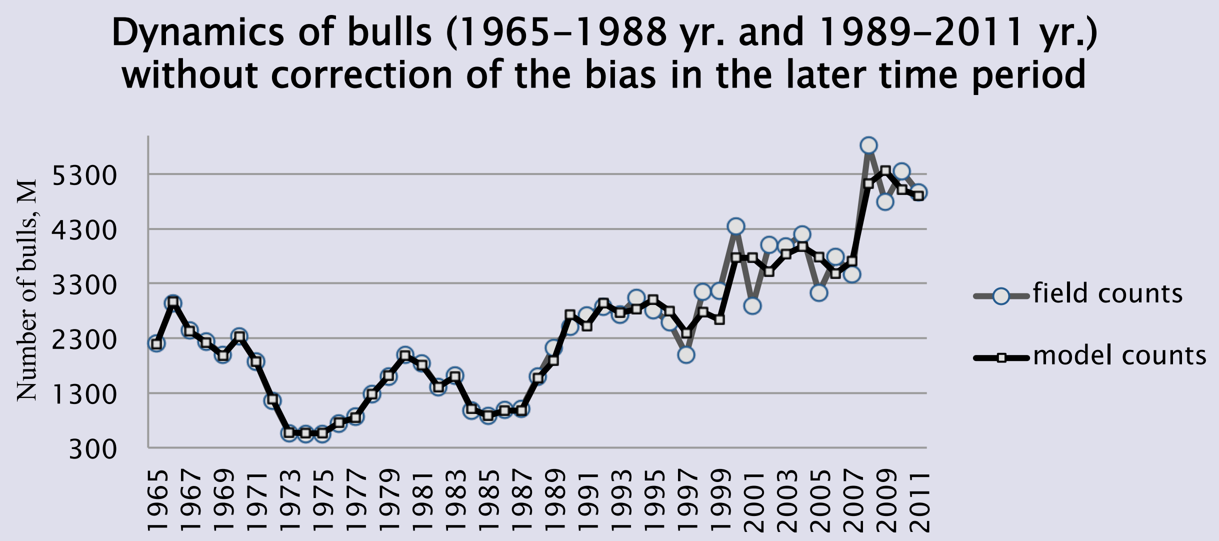
- 1989-2013 yr.:

$M(n) - M_7(n) = 0.48 \cdot (M(n-1)-R(n-1)) + 5.35$

  - R^2=0.91
  - The intercept is unsignificant (p=0.96), i.e. the estimate M_7 has not a bias

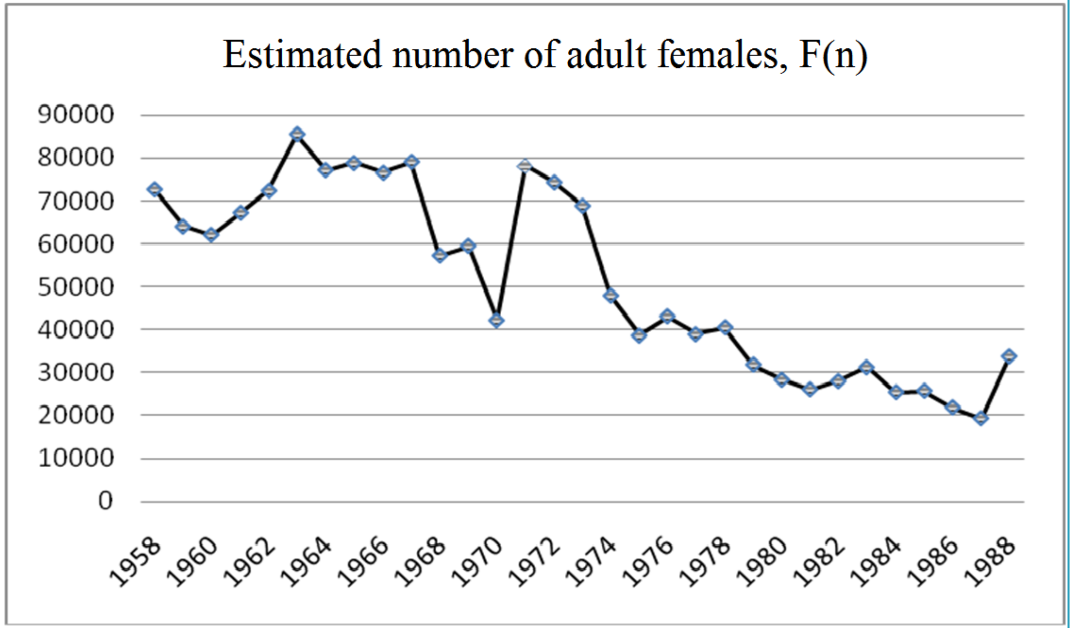
- The main assumptions of OLS are hold.
- Average error of approximation is A=3.2%.

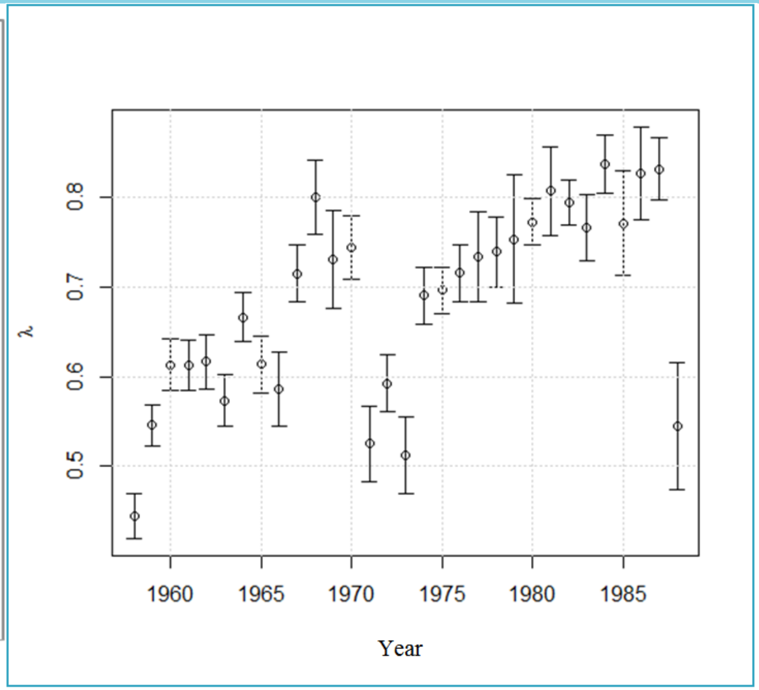




Estimating the survival rates for fur seal females of different ages on the base of observations data. Age structure dynamics in female component of the herd (1 from 2)

- The pregnancy rates were calculated from the data about physiological state of females from marine samples:
- $\lambda(n) = f^*(n)/f(n)$
  - Here $f(n)$ is the size of marine sample of n-th year, and $f^*(n)$ – the number of pregnant females in this sample.
  - Normal approximation was used for the 95%-confidence interval calculation $\lambda \pm \sigma_\lambda \cdot t_\beta$, here $\sigma_\lambda = \sqrt{\lambda(1-\lambda)/n}$ is standard deviation.
- Following previously developed procedure (Frisman et. al., 1982), adult females number is $F(n) = P(n)/\lambda(n)$





Estimating the survival rates for fur seal females of different ages on the base of observations data. Age structure dynamics in female component of the herd (2 from 2)

- Following previously developed procedure (Frisman et. al., 1982):
- The size of female cohort of age i-yr in n-th yr:

$$F_i(n) = F(n) \cdot f_i(n) / \sum_j f_j(n)$$

- The survival rate of females from birth to 3 yr, for pups, that were born in n-th yr:

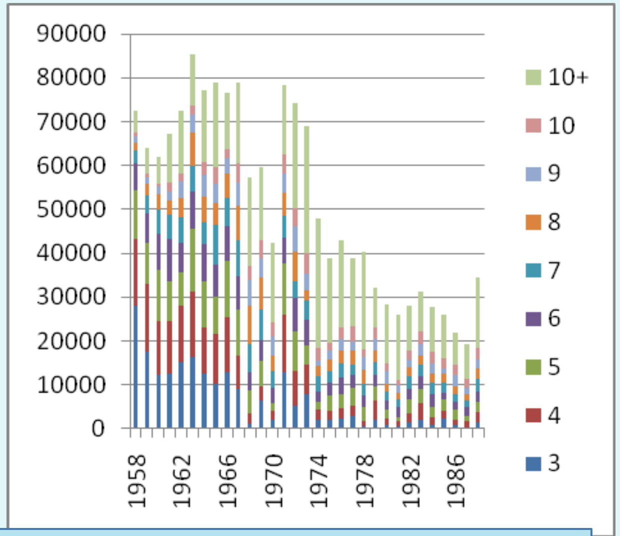
$v_{03}(n) = F_3(n+3)/(P(n)/2)$.

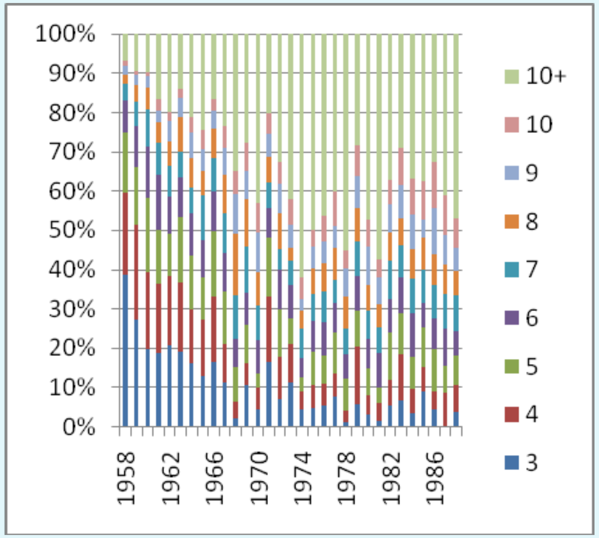
- Average survival rate of females between i-th and j-th yr:

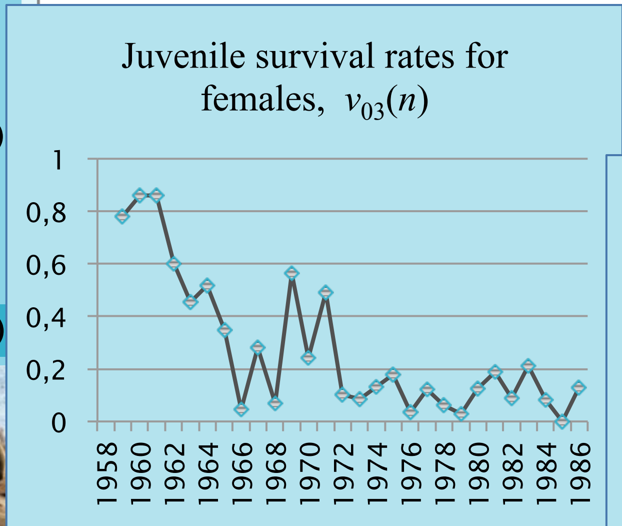
$$v_{i,i+1} = \sum F_{i+1}(n+1) / \sum F_i(n)$$

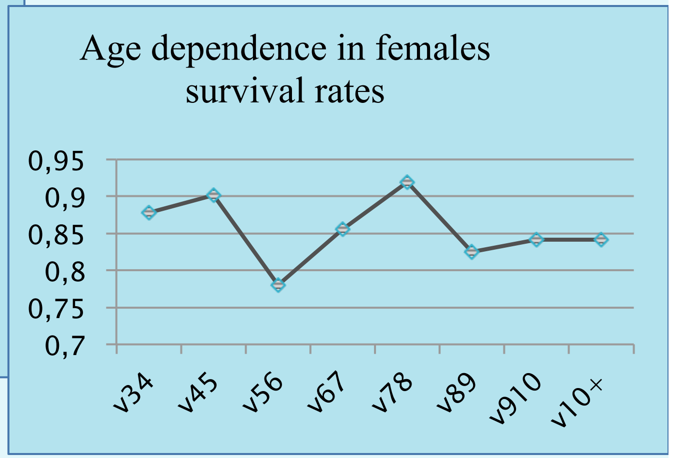
- Average survival rate of females from birth to 3 yr:

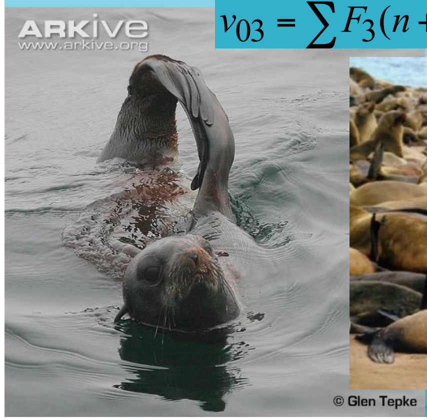
$$v_{03} = \sum F_3(n+3) / \sum (P(n)/2)$$











The model:

$$2F_0(n) = P(n);$$

$$F_3(n-1) = v_{03}F_0(n-3);$$

$$F_{i+1}(n) = v_{i,i+1}(n-1)F_i(n-1), \quad i = \overline{3,9};$$

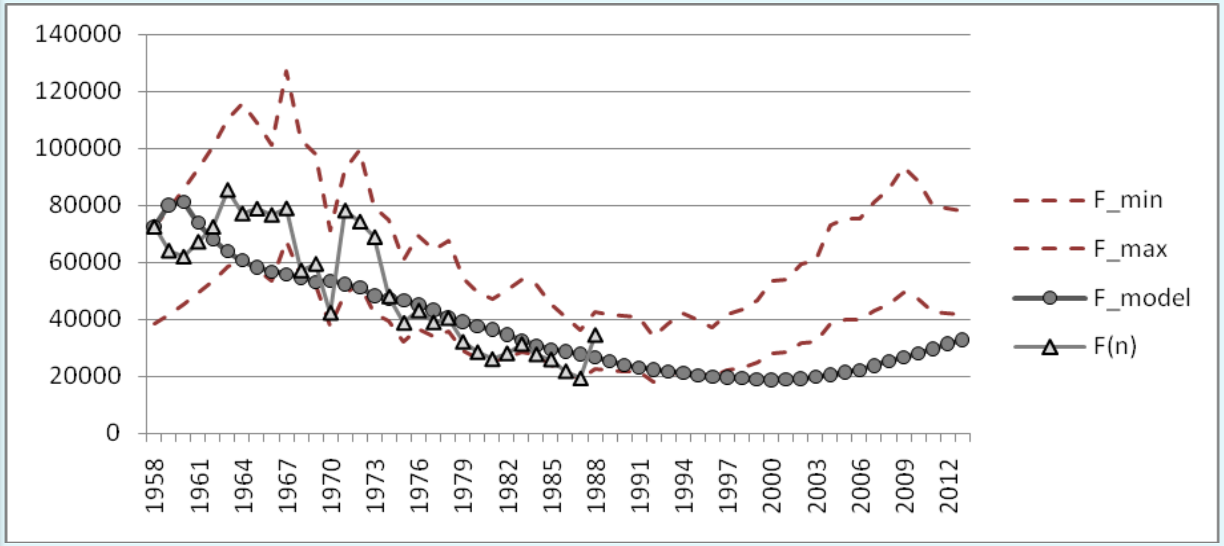
$$F_{11}(n) = v_{10,11}F_{10}(n-1) + vF_{11}(n-1);$$

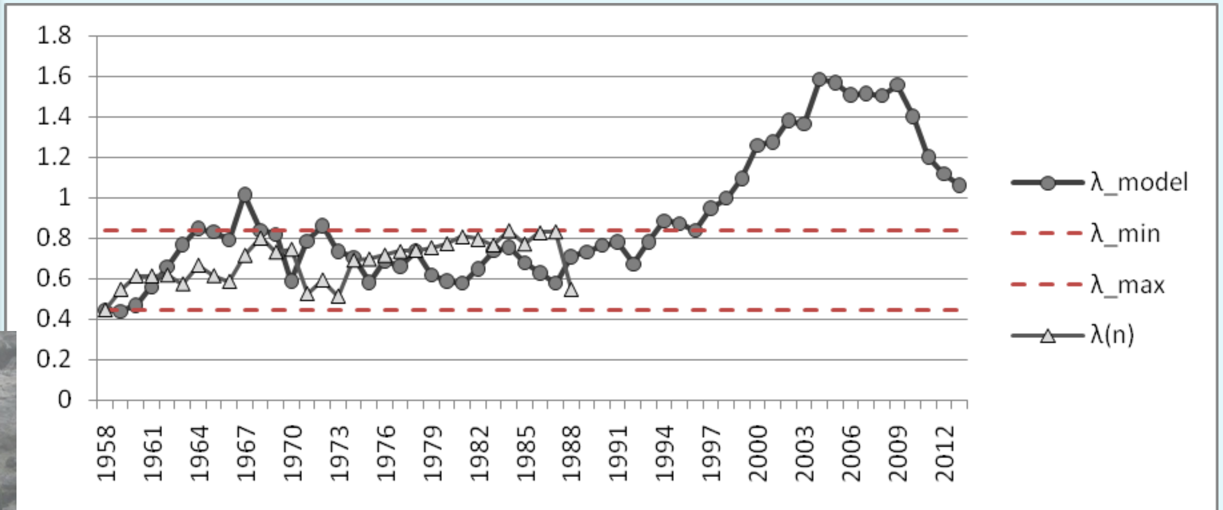
- The observations of pups number ($P/2=F_0$), and rates calculated v_i are utilized in the model

- The reasonable limits for adult females number:

$$F_{max}(n) = P(n)/\lambda_{min}$$
$$F_{min}(n) = P(n)/\lambda_{max},$$

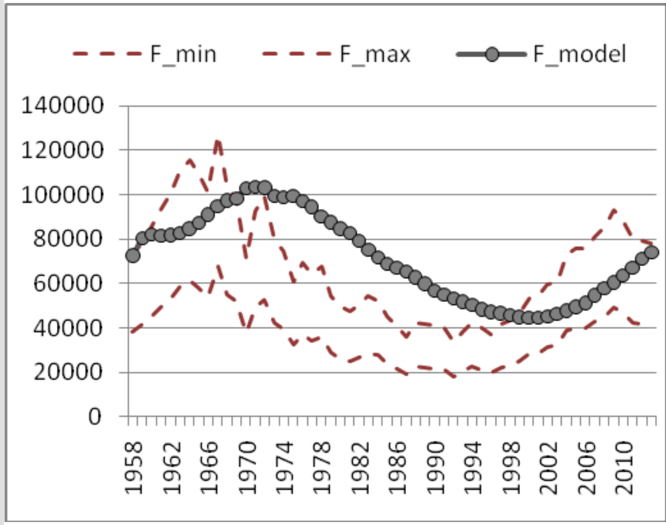
From data set (1958-1988 yr): $\lambda_{min} = 0.44$ and $\lambda_{max} = 0.84$.

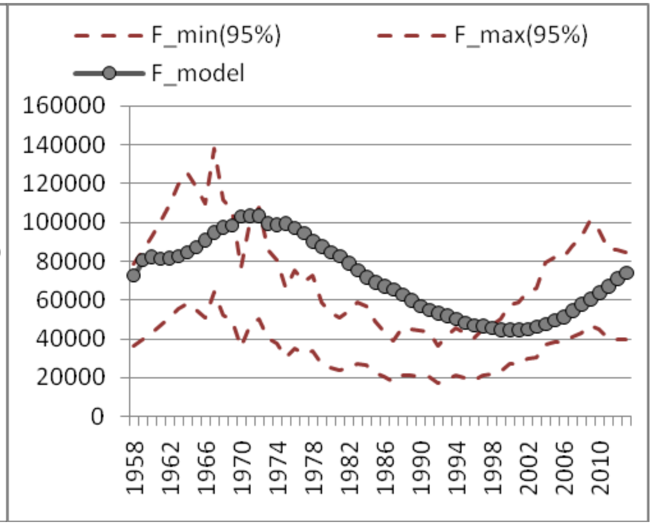


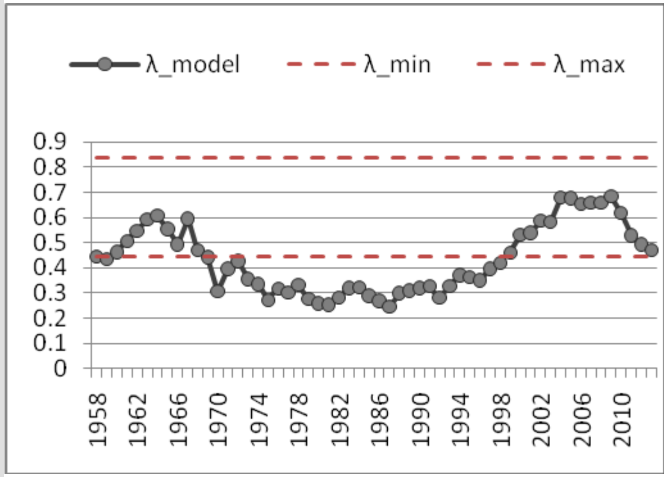


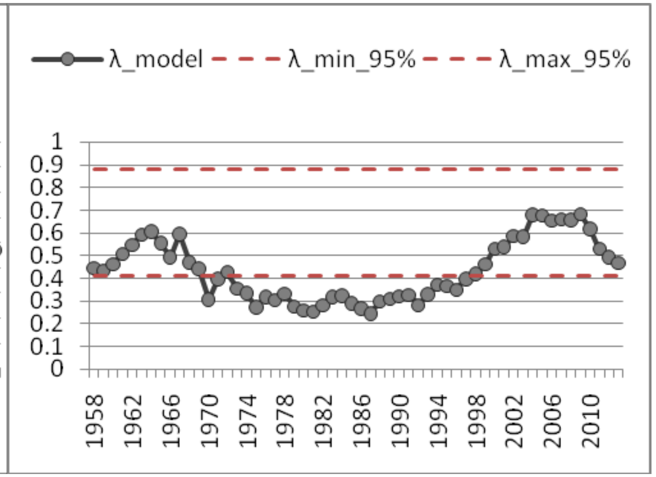
Searching for the values of survival rates giving dynamics of adult females number that is consistent with the dynamics of pups born

- <u>The aim</u> – calculated pregnancy rate is in reasonable interval: $0< \lambda <1$
- <u>The assumptions</u>
  - Survival rate for adult females (for ages from 3 yr. to 10 yr.) is constant;
  - For old females with age after of 10 yr. this parameter reduces due to natural aging
  - And minimal survival rate has juvenile group (from birth to 3 yr.)
- <u>The optimization criteria</u> :
  1. Minimization of calculated numbers of adult females, that are outside the “reasonable interval” ($F_{min}(n)$, $F_{max}(n)$);
  2. Minimization of calculated pregnancy rates with low-probability:
     - searching for minimum of penalty function;
     - values of $\lambda(F)$ out of 95%-confidence interval have a penalty, that is inversely proportional to the probability to obtain this value.







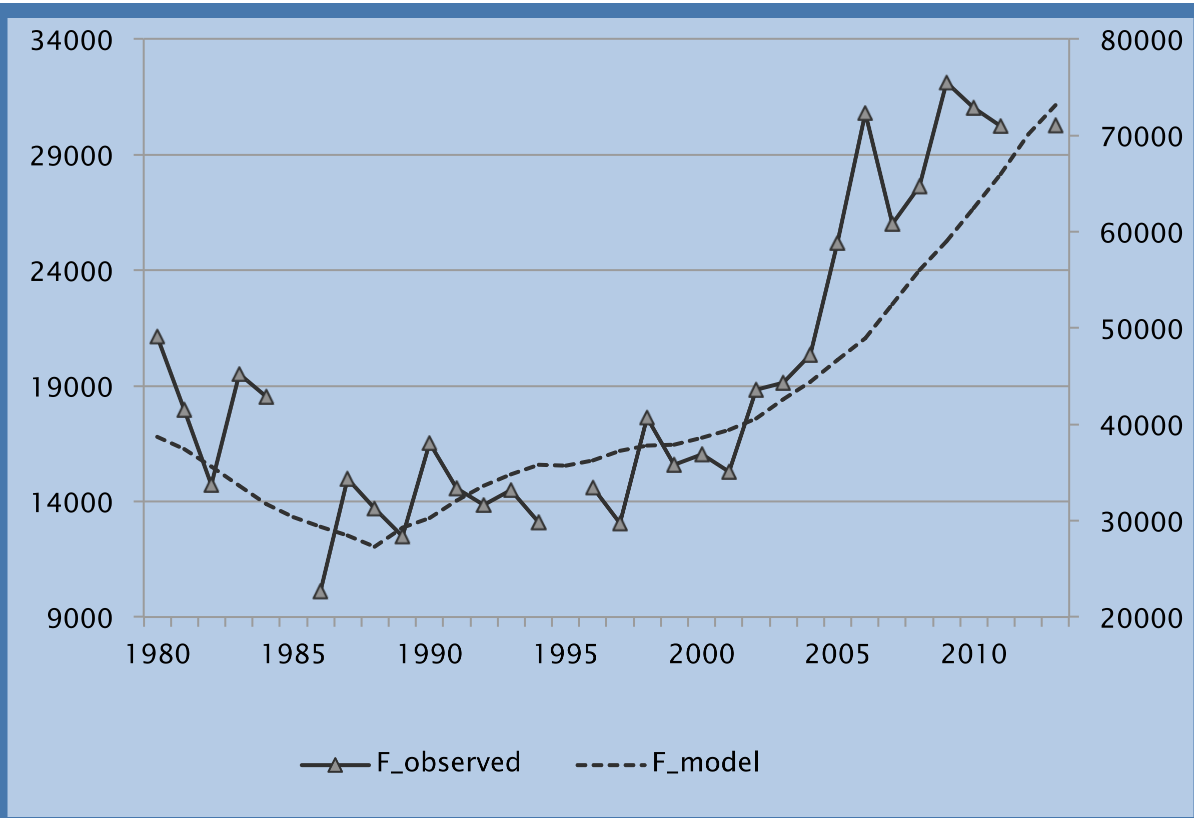


<u>The result:</u>
In the early period (before 90th yr.) the new coefficients give overestimated number of females and, as a consequence, the calculated pregnancy rate falls below the low boundary; and later - the number of females goes down to the lower limit (apparently, it is understated), which confirms the assumption that the change of females survival occur after 1988 yr.

Searching for the values of survival rates; separation for two periods

- The survival rates calculated from data for early period (1958-1988 yr.) are implemented into the model for this period;
- New parameters (v_i) were searched only for later time period (1989-2013 yr.) with previously described optimization criteria:
  I. There are a set of satisfactory results, i.e. calculated number of adult females $F(n)$ lies inside the reasonable limits ($F_{min}(n)$, $F_{max}(n)$) during all late period;
  II. There are a set of satisfactory results, where calculated pregnancy rates lies inside the 95%-c.i.

- The set of satisfactory results has
  - Minimal value of females juvenile survival $v_{03} = 0.465$ (that is considerably higher than those from the data of marine samples: 0.29), and maximal value is $v_{03} = 0.67$.
  - Various values of survival rates for older ages: more and less than average value from the data (1958-1988 yr.).



Dynamics of adult females number observed on the rockery (left scale) and its model number (right scale). The model parameters are following: $v_{03} = 0.625$, $v_{34}=v_{45}=\ldots v_{910}\approx 0.87$, $v_{10+}=0.86$.

Results: One can conclude, that females juvenile survival (from birth to 3 yr, v_{03}) had to increase to give the observed number growth of pups born after prolonged depression.

Conclusion

- For estimating the juvenile survival rate of male fur seals the Lander method and its modifications were used.
  - It was found that this methodology does not work properly in the late period (after end of 1980s) due to the changes in the harvesting the population.
- Satisfactory estimates for all characteristics of males' lifecycle have been gained.
- It was revealed that structural change of its survivability occurred at the end of 80s
  - i.e. survival of subadult and adult males increased slightly.
- New estimates of survivability rates give the model dynamics of the bulls number, which is in good agreement with the observed one
  - its mean error of approximation equals 3.2%.
- A set of numerical simulations shows, that juvenile survival rate of females had to increase too to be able to give an adequate dynamics of adult females' number

Problems :

1. Has been solved: the model parameters are estimated

And the Cause of slow and uncertain population growth is not a sharp reduce in survival rates of juveniles or other age groups

The next problems:

2. Correcting the general model
    - Testing the existence of a density dependence effects in juvenile survivals
    - Influence of sexual ratio in the population on females' pregnancy rates
    - Understanding the evolutionary consequences of the harvest: was it really unselective one, that did not force the bulls to grow weak?

3. Constructing the more accurate the forecast and the management strategy

Photo from http://komandorsky.ru/callorhinus-ursinus-linnaeus.html
c. Eugenii Mamaev

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