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On a Feasible Formal Description of the Natural Mortality Rate Variation in
Relation to Age of Beaked Redfish and Capelin from the Northwest Atlantic

by

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ABSTRACT

Variation of the natural mortality rate with age of beaked redfish from Divs. 3MLN and capelin from Divs. 2J+3K and 3LNO is described by a convex down one minimum function tending to infinity when the age tends to maximum possible which may be attained by fish under actual ecological conditions in the absence of fishery. A method of estimating this function's parameters is suggested and checked. Estimates of the natural mortality rate are presented for redfish aged 5 to 23 years and capelin at age 2 to 6 years.

INTRODUCTION

Modern ecology (Vilee, Dethier, 1974; Odum, 1975) recognizes five theoretically possible types of survival curves (Fig.1). It is hypothesized that during the life time from egg to mean age of mature fish (t_c) the survival curve is concave downward and it is convex upward at subsequent stages (Nikolsky, 1974). Accordingly, the survival curves of beaked redfish from Divs. 3LNM and Newfoundland capelin appear to be close to the fourth type. The results of age determinations of unexploited and scarcely exploited fish give an idea of the survival curve behaviour only within the interval $[t_c', t_2]$, where t_c' - age at which all fish are exploited, t_2 - maximum age of fish in industrial stock. The survival curve shape in the interval $[t_2, t_c']$, where t_2 is the age of recruitment, may be illustrated only when the numbers of age groups pertaining to this interval are known.

Fig. 2 shows the catch curves for some fish species from the Northwest Atlantic. The curves represent age composition of each species in catches in the early years of fishery. To eliminate fluctuations of yearclass abundance the results of age determinations of fish from every industrial stock are combined for a series of years during which the fishing was not intensive and also smoothed by a running average of three. These curves together with catch curves for a number of freshwater fish populations (Ricker, 1958) indicate that from a certain age $t > t_c'$ the approximated survival curves are convex upward and diminish. This means that there is an age in the interval $[t_c', t_\lambda]$ beginning from which the natural mortality rate of those populations increases.

In 1961 under the guidance of E.B. Burmakin a unique experiment was conducted (Rudenko, 1967). The eutrophic Somino Lake (Pskov Region) with an area of 21.4 hectares was poisoned with polychlorpinene. Three years prior to this a traditional intensive fishing in the Lake had been closed. Straight-forward counting had given the numbers of age groups of 11 species inhabiting the Lake beginning from age 1+. The analysis of derived age compositions showed that the survival curves in the interval $[1+, 3+]$ were convex downward and decreased which meant that the natural mortality rate in this interval was reduced.

Hence, both Fig. 2 and information from the literature evidence that in the interval $[t_2, t_\lambda]$ the approximated survival curves for some unexploited or scarcely exploited fish species may look like a monotonic decreasing function with, at least, one inflection point. Therefore, the natural mortality rate may be represented by an age function with one (positive) minimum and becoming infinite at t tending to age t_c , which, in case of unexploitation, corresponds to the maximum possible lifetime of fish under actual ecological conditions.

This paper considers one feasible formal description of the natural mortality rate variation in the interval t_2 to t_λ .

MATERIAL AND METHODS

Let us assume that the rate of M variation is directly propor-

tional to the ratio of $(t - \bar{t}_s)$ to $(t - t_e)$;

$$\frac{dM}{dt} = a \frac{t - \bar{t}_s}{-(t - t_e)} \quad (1)$$

Then the variation of the natural mortality rate of fish from every yearclass in the interval (t_e, t_e) may be described by the formula:

$$M(t) = a [-t - (t_e - \bar{t}_s) \ln(t_e - t)] + b. \quad (2)$$

This function is defined, continuous and has a single stationary point \bar{t}_s in the considered interval; with $a > 0$ $\min M(t) = M(\bar{t}_s)$. Assuming that the function minimum $M(t)$ conforms with the mean age of mature fish (Nikolsky, 1974), \bar{t}_s and t_e have a concrete biological meaning. Whereas parameters a and b are of no biological meaning.

There is a peculiarity in the function $M(t)$ at $t = t_e$, however, the integral $\int_{t_e-1}^{t_e} M(t) dt$ converges. Therefore, it may appear that some individuals exceed the limit age. To exclude this case let's generalize the formula

$$(1): \frac{dM}{dt} = a \left[\frac{t - \bar{t}_s}{t_e - t} + \gamma \frac{t - \bar{t}_s}{(t_e - t)^2} \right], \quad \gamma \geq 0,$$

then we have

$$M(t) = a [-t - (t_e - \bar{t}_s - \gamma) \ln(t_e - t) + \gamma \frac{t_e - \bar{t}_s}{t_e - t}] + b, \quad (3)$$

where γ - a parameter with no biological meaning. The estimation of a , b and γ is hampered by introduction of one more parameter in the formula $M(t)$. Calculations show that at $0 \leq \gamma < 1$ natural mortality rates derived from formulae (2) and (3) are equal to within 0.01, and scanty fish survive to the age $t_e - 1$. Therefore, γ is accepted equal to 0.

The form of the function $M(t)$ also will not change for heavily fished stocks. Merely its parameters will change, probably according to the intensity and pattern of fishery and other ecological conditions. The effect of different factors depending on density and limiting fish numbers will grow weaker, so the natural mortality of fish will decrease (Bukhanevich, 1973; Odum 1975; Sergeev, 1979; Pianka, 1981). This will entail the increase in t_e which will tend in this case to the age equal to the maximum possible physiological lifetime. For the first approximation t_e may be assumed

to be constant and it is usually known. \bar{t}_s will decrease. It may be easily estimated from fishing and biological statistics.

To estimate a and b two different values with known $M(t)$ should be available in the interval $[t_2, t_e]$. This requirement is fulfilled in exceptionally rare cases. Therefore, let's assume that under conditions of exploitation so intensive that the area contains few fish older than t_λ'' (where $t_\lambda \leq t_\lambda'' < t_e$), there is an age t_m or an interval $[t_1, t_2]$ for which the natural mortality presumed to be constant may be estimated using known methods. Commonly, the relation $t_e' \leq t_1 \leq t_m \leq t_2 \leq t_\lambda$ and equation $N(t_\lambda'' + 1) = 0$ are valid.

Let's assume further that fish which are to die from fishing will die only for natural reasons in accordance with the function $M(t)$. In this case the equation $N(t_\lambda'' + 1) = 0$ is invalid because some of these fish will survive to age t_e . We shall assume that the abundance of this cohort of fish at age $t_e - 1$ meets the inequality:

$$N(t_e - 1) > 1; \quad (4)$$

At age $t_e - 1$ the number of these fish will constitute

$$\sum_{\tau=t_2}^{t_\lambda''} c_\tau \exp \left\{ - \int_{\tau}^{t_e-1} M(t) dt \right\}, \quad (5)$$

where c_τ is the number of individuals captured at the age τ (τ is equal to the whole part of t and coincides with a start of a respective calendar year). Fish, which under fishing conditions have died for natural reasons, will now survive to age $t_\lambda' < t_\lambda''$.

Equation (5) contains two unknown parameters a and b which should meet the requirements that $a > 0$ and $\min M(t) > 0$, so that the inequality (4) is obtained.

If the natural mortality rate is known at point t_m (let M_{t_m} represent it) then bearing (2) in mind we get

$$b = M_{t_m} + a [t_m + (t_e - \bar{t}_s) \ln (t_e - t_m)]. \quad (6)$$

If the natural mortality rate is only known for the interval $[t_1, t_2]$ (let \bar{M} represent it) then after finding b from

$$\bar{M} = \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} M(t) dt, \quad (7)$$

we have

$$b = \bar{M} + \frac{a}{2} (t_2 + t_1) - a \frac{t_e - \bar{t}_s}{t_2 - t_1} [(t_e - t_2) \ln(t_e - t_2) - (t_e - t_1) \ln(t_e - t_1) + (t_2 - t_1)] \quad (8)$$

Estimates M_{tm} and \bar{M} are supposed unbiased.

In the formula

$$\mu = \frac{1}{t_e - t_2 - 1} \int_{t_2}^{t_e-1} M(t) dt,$$

where μ is the mean natural mortality rate in the interval t_2 to t_e-1 , we substitute for the right parts of equations (6) and (8) for (8) and have: in the first case

$$a = \frac{\mu - M_{tm}}{t_m + (t_e - \bar{t}_s) \ln(t_e - t_m) - 0,5(t_2 + t_1) - \frac{(t_e - \bar{t}_s)(t_e - t_2) \ln(t_e - t_2) + (t_e - \bar{t}_s)}{t_e - t_2 - 1}} \quad (9)$$

and in the second

$$a = \frac{\mu - \bar{M}}{\frac{t_2 + t_1}{2} - \frac{t_e - \bar{t}_s}{t_2 - t_1} [(t_e - t_2) \ln(t_e - t_2) - (t_e - t_1) \ln(t_e - t_1) + (t_2 - t_1)]} \quad (10)$$

$$- \frac{1}{\frac{t_e + t_2 - 1}{2} - \frac{t_e - \bar{t}_s}{t_2 - t_1 - 1} [(t_e - t_2) \ln(t_e - t_2) - (t_e - t_2 - 1)]}$$

Believing that $M(t) = \text{const} = \mu$ we find that the abundance $N(t)$ of a yearclass at any given age $t_2 \leq t < t_e$ in the absence of fishery will amount to

$$N_{t_2} \cdot \exp \{-\mu \cdot (t - t_2)\}.$$

Presenting the yearclass biomass at age t as

$$P(t) = N(t) \cdot w(t),$$

where $w(t) = a_1 \cdot b_1 \left\{ 1 - \exp(-\kappa(t - t_0)) \right\}^{b_1}$ - the von Bertalanffy equation which shows the fish weight increment, a_1 and b_1 - parameters of the allometric growth equation, we find that the yearclass biomass at age t_3 will be the maximum, if

$$b_1 \kappa \exp \{-\kappa(t_3 - t_0)\} - \mu \left\{ 1 - \exp(-\kappa(t_3 - t_0)) \right\} = 0.$$

whence it follows that

$$\mu = \frac{b_1 \kappa}{\exp[\kappa(t_3 - t_0)] - 1}$$

Substituting the right part of the last equation for μ in formulae (9) and (10) and using the scanning method (Rastrigin, 1974) with revised t_3 , we shall easily determine the parameters a and b complying with all requirements.

The method allows to estimate theoretically the natural mortality rate for each yearclass. Unfortunately, we can not determine the mean age of mature fish for each separate yearclass, therefore, we are compelled to accept \bar{t}_s equal for all yearclasses.

Table 1 presents estimates of all parameters required in estimation of a and b in the function M(t) for beaked redfish from both areas and Newfoundland capelin. Table 2 shows the mean number of captured fish from each age group. For both species von Bertalanffy's equation parameters were estimated using the method of Hohendorf (Hohendorf, 1966) and those of allometric growth equation - the least squares technique. For beaked redfish the mean age of mature fish, growth equation parameters and mean number of captured fish at age were determined from age determination results and catch statistics for 1968-1984 and for capelin - 1973-1984. The natural mortality rate of capelin of 3-4 years of age was accepted equal to 0.30. For beaked redfish aged 5 to 23 years the lowest values of the mean natural mortality rate were selected, at which the function M(t) at point \bar{t}_s is above 0.01.

RESULTS

Table 1 presents estimates of a and b in the function M(t) for beaked redfish and capelin. For beaked redfish from Divs. 3LN the function has the form:

$$M(t) = 0,1124[-t - 19 \ln(30-t)] + 7,5402,$$

from Div. 3M:

$$M(t) = 0,1183[-t - 18 \ln(30-t)] + 7,5853,$$

and for capelin:

$$M(t) = 1,4101[-t - 5 \ln(9-t)] + 17,2450.$$

Fig. 3 illustrates these functions.

Estimates of the natural mortality^{rate} of beaked redfish from both areas are close to the generally accepted value of 0.10 only at age 5. The mean natural mortality rate in the interval 5 to 23 years is 2.3 times higher than 0.10. By 17 years this rate reaches 0.10 and then sharply rises approaching 1 at last fishing age. (Table 3).

The suggested method in an integral form allows for a death of post-spawners, however, it is impossible yet to evaluate this phenomenon quantitatively. This is a weak point of the method, as far as capelin is concerned. Nevertheless, we thought it feasible to use it, because we believe that within all assumptions, requirements and restrictions we have succeeded in estimating the natural mortality rate of capelin of each fishing age.

Certain divergencies from estimates derived earlier (Bakanev,

Lugovaya, Tretyak, 1985; Nikolskaya, Savateeva, Tretyak, 1985) are due to the fact that the coefficients a and b have been estimated with additional requirements:

$$N(t_e) \geq 1 \quad \text{and} \quad N(t_e+1) < 1,$$

which are disregarded now.

The suggested method allows to estimate the natural mortality rate of fish from all age groups of the industrial stock, this estimate may be used as an input parameter in the VPA.

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Table 1. Parameters used for estimation of the natural mortality rate of beaked redfish from Div. 3MLN and capelin from Divs. 2J+3KLNO. Estimated coefficients a and b.

Parameter	Species		
	Beaked redfish		Capelin
	Div. 3M	Divs. 3LN	Div. 2J+3KLNO
t_e	30	30	9
\bar{t}_s	I2	II	4
K	0,066	0.06I	0.356
t_o	-2.570	-2.090	-0.667
b_1	3.160	2.960	3.284
t_m	5-23	5-23	3-4
\bar{M}	0.150	0.170	0.300
a	0.1183	0.1124	1.4101
b	7.5853	7.5402	17.2450

Table 2. Mean number of beaked redfish captured in 1968-1984 and capelin in 1973-1984 at different fishing age, thou.individuals

τ , years	species		
	Beaked redfish		Capelin
	Div. 3M	Divs. 3LN	Divs. 2J+3KLNO
2			163655
3			1936111
4			2641088
5	405	3030	1209238
6	835	4172	209274
7	1897	3793	
8	2875	4666	
9	3905	4332	
10	4977	5002	
11	4759	3522	
12	3496	3433	
13	3337	2569	
14	2730	1809	
15	2196	1701	
16	1717	1116	
17	998	622	
18	732	785	
19	598	748	
20	421	2032	
21	293	601	
22	125	526	
23	54	285	

Table 3. Natural mortality rates of beaked redfish from
Divs 3MLN and capelin from Divs. 2J+3KLNO
at different fishing age

τ , years	Species		
	Beaked redfish		Capelin
	Div. 3M	Divs. 3LN	Divs.2J+3KLNO
2			0.71
3			0.38
4			0.26
5	0.14	0.10	0.42
6	0.11	0.08	1.04
7	0.08	0.06	2.49
8	0.06	0.04	
9	0.04	0.03	
10	0.02	0.02	
11	0.01	0.01	
12	0.01	0.02	
13	0.01	0.03	
14	0.03	0.04	
15	0.04	0.07	
16	0.07	0.11	
17	0.11	0.15	
18	0.16	0.21	
19	0.23	0.28	
20	0.32	0.37	
21	0.42	0.49	
22	0.56	0.63	
23	0.72	0.80	

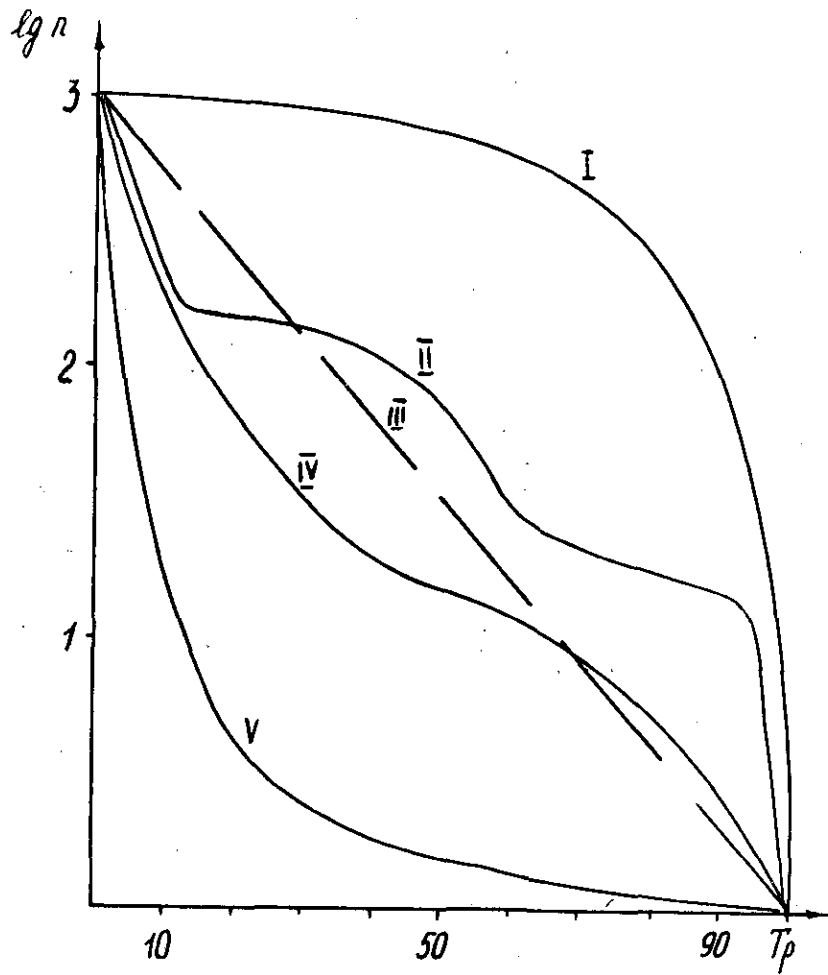


Fig.1 Types of the survival curve (I-V)
 T_p - % of the maximum possible life span;
 $lg n$ - abundance index.

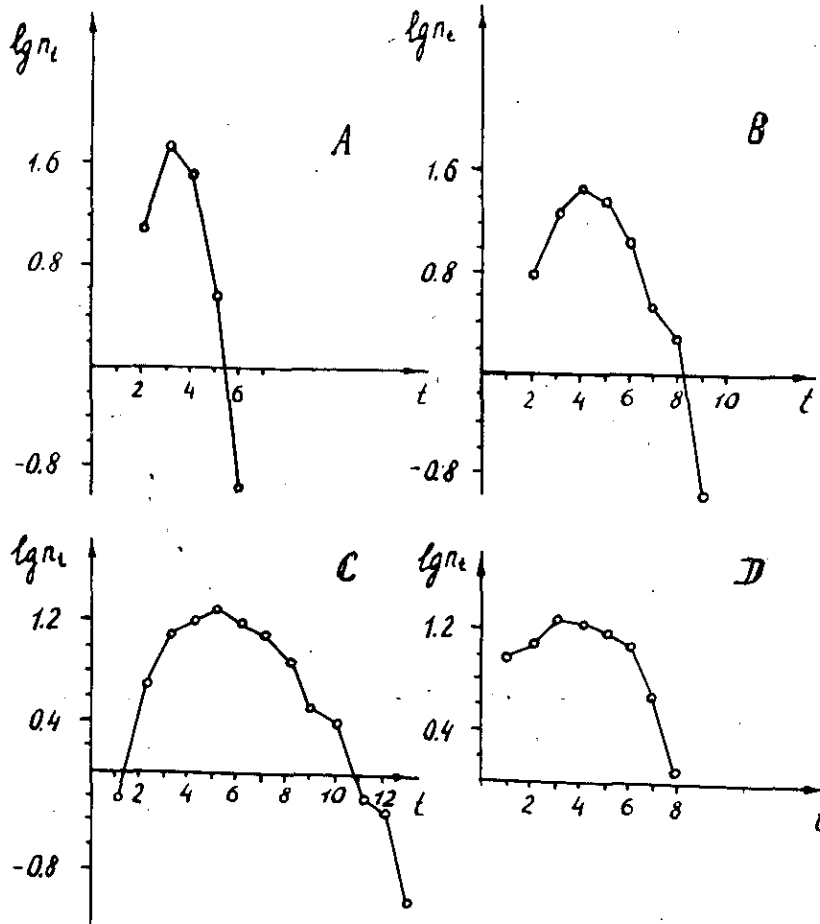


Fig. 2 Catch curves for Newfoundland capelin (A), Barents Sea polar cod (B), blue whiting (C) and beaked redfish of the Bear Island-Spitsbergen population (D) in early years of exploitation.

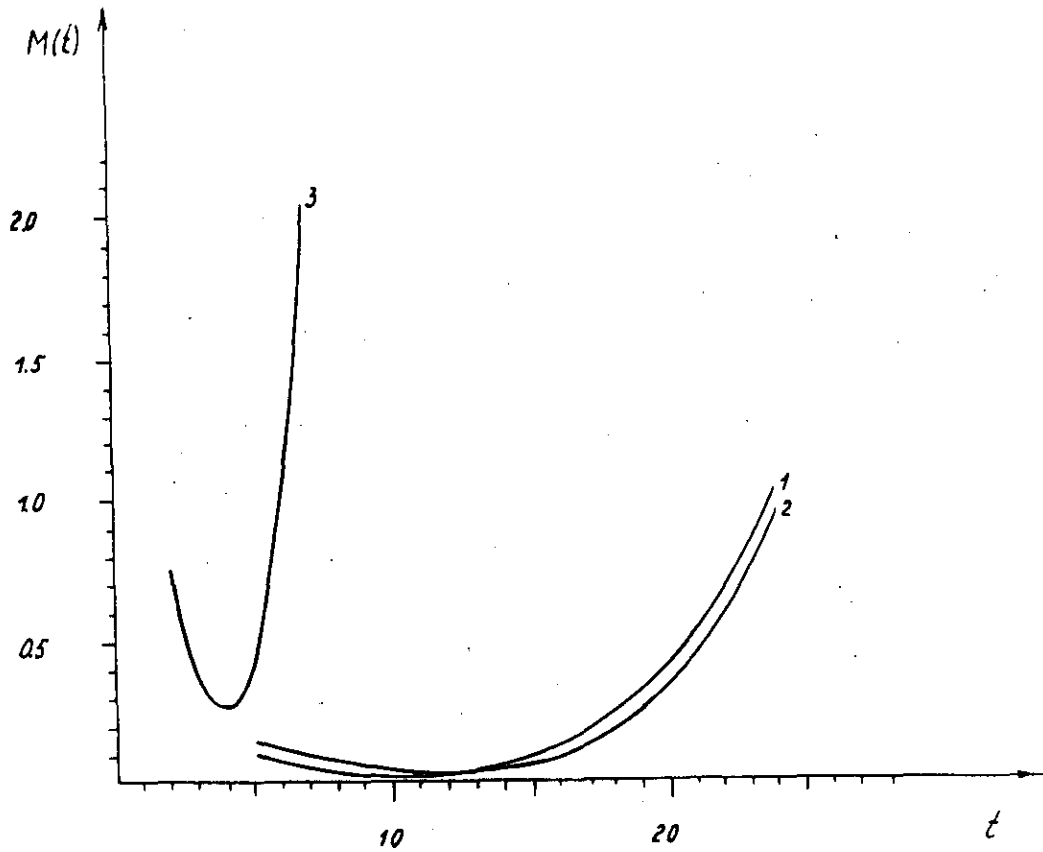


Fig. 3 Function $M(t)$ for beaked redfish from Div. 3M (curve 1); from Divs. 3LN (curve 2) and capelin from Divs. 2J+3K and 3LNO (curve 3).