

**Modelling of age-dependent instantaneous coefficients of natural mortality for
Northeast Arctic cod**

by
V. L. Tretyak

Polar Research Institute of Marine Fisheries and Oceanography (PINRO), 6,
Knipovich Street, 183763, Murmansk, Russia

Abstract

Natural mortality coefficients used to assess the commercial cod stock are presently taken to be identical ($M=0.20$) for almost all age groups of this stock. The paper describes a model suggesting that instantaneous coefficients of natural mortality change with age increasing from 3 years and further. The model explicitly reflects a conceptual relationship between natural mortality of cod, maturity age and theoretical maximum possible lifetime, and implicitly - between natural mortality, linear and weight growth. Theoretical premises of the model are formulated and a method of estimating its parameters is suggested. Natural mortality coefficients are calculated for cod from 1946- 1991 yearclasses at the age of 3 years and older. To calculate terminal values of coefficients mean weight of one fish at a particular age and the mean of average yearly water temperature in the main branch of the Murman Current in the 0-200 m layer in the first three years of generation life was used. The coefficients can be applied for assessment of the total and spawning stocks, setting up of biological reference points and total allowable catch.

Introduction

The curves of survival of fish not subject or nearly not subject to the fishery have a shape of monotonously diminishing function with one point of bend. This means that beginning from a certain age the instantaneous coefficient of fish natural mortality can be presented by a function of their age $M(t)$ having one (positive) minimum in a point corresponding to a bend point on the survival curve (Tretyak, 1984). This function has either clearly expressed or a wide domain of minimum. The paper suggests function $M(t)$ and its two components, a method to assess function parameters, the instantaneous coefficients of cod natural mortality of 1946- 1991 year classes at age 3 and more are calculated, and the analysis of their variability is done.

Materials and methods

To describe changes of instantaneous coefficients of cod natural mortality a

mathematical model - an ordinary differential equation of the first order - is suggested. The function $M(t)$ is a solution to this equation. The quantitative information on age at 50% maturity, length and weight growth, as well as on the abundance of a virtual population at the age of 3 was required. For 1946-1976 year classes, age at 50% maturity was calculated based on data from Jorgensen (1990), whereas for 1977-1991 year classes - on data from the Arctic Fisheries Working Group (Anon., 2000). Mean length and weight of cod of 1985-1991 year classes at the age of 3-9 were determined by results of Russian and Norwegian surveys (Anon., 2000). Length and weight growths of cod of 1946-1984 year classes were reconstructed by using the equations of the relationship between length and weight of cod in the southern Barents Sea (Ozhigin et al., 1994-1996) and the corresponding indices of growth obtained by summarized results of Russian and Norwegian surveys. The abundance of the virtual population of cod was taken from materials of the ICES Arctic Fisheries Working Group (Anon. 2000).

Model premises

The causes of cod natural mortality are divided into two conditional categories. The first one includes the causes of exogenous origin determined by the environmental conditions under which cod dwell, they are: unfavourable abiotic conditions exceeding the tolerant possibilities of an organism the food deficiency, cannibalism and the influence of parasites and predators. The second category includes the causes of the endogenic origin determined by the abundance, structure and adaptive abilities formed during the evolution: diseases, postspawning stress, metabolic, disorder and others. The analysis of biological and ecological features of cod natural mortality (Borisov and Shatunovsky, 1973; Borisov, 1978a; Tretyak et al., 1989; Korzhev and Tretyak, 1989; Tretyak et al., 1991; Eiyaid et al., 1992; Korzhev and Tretyak, 1992; Dolgov et al., 1995; Korzhev et al., 1996; Ponomarenko and Yaragina, 1996; Anon., 1996; Dolgov, 1997; Dolgova and Dolgov, 1997; Dolgov, 1999; Ozhigin et al., 1999; Tretyak et al., 1999; Anon., 2000), allows to assume that with age the effect of exogenous causes, except parasitism, becomes weaker, whereas that of endogenic causes becomes stronger. This means that with increasing cod age the additive component in the natural mortality function ($M_1(t)$) caused by exogenous factors, except parasites, is declining while that caused by endogenous factors and parasites ($M_2(t)$) is increasing. In the first approximation we assume that a variation rate of the first component becomes slower and that of the second becomes faster. General view of functions $M_1(t)$, $M_2(t)$ and $M(t)$ is given in Fig. 1.

$M(t)$ denote the instantaneous coefficient of the generation natural mortality, equal to a sum of $M_1(t)$ and $M_2(t)$, at the moment of time t ($t \geq t_r$, where t_r - the age of the commercial stock recruitment, $t_r=3$ years) and $M(t+\Delta t)$ - at the moment of time $(t+\Delta t)$. The difference

$$\Delta M = M(t + \Delta t) - M(t) \quad (1)$$

will present the increment of function $M(t)$ over the time interval from t to $(t+\Delta t)$. This increment is attributable to interaction of natural mortality causes from both categories. It will diminish under the influence of exogenous causes, except parasites, over the time Δt , and it will increase under the influence of endogenous causes and parasitism. Therefore, the increment of function $M(t)$ is presented as a sum of two summands:

$$\Delta M = \Delta M_1 + \Delta M_2, \quad (2)$$

where ΔM_1 - increment caused by the external reasons, except parasites;

ΔM_2 - the increment caused by internal reasons and parasitism.

Apparently, the increment ΔM_1 is negative and depends on the time interval Δt : the larger Δt , the larger $|\Delta M_1|$ is. Besides, it depends also on the age t : the larger t , the quicker the weakening of the effect of exogenous causes is and, hence, $|\Delta M_1|$ is less. Taking into account that with increasing age t the time interval (t_e+1-t) left for the fish to live decreases, where t_e is theoretical maximum possible lifespan, it can be stated that $|\Delta M_1|$ is directly proportional to this interval:

$$|\Delta M_1| = \frac{a_1}{t_s} \cdot \frac{(t_e+1-t)}{t} \cdot \Delta t, \quad (3)$$

where t_s - cod age which is fully determined by biological and ecological features of a population, year;

a_1 - coefficient of proportionality, year⁻¹.

Thus, ΔM_1 is a function of two variables Δt and t :

$$\Delta M_1 = -\frac{a_1}{t_s} \cdot \frac{(t_e+1-t)}{t} \cdot \Delta t. \quad (4)$$

It is negative and decreases with increasing Δt , it increases with increasing age t , it is equal to zero at $\Delta t=0$ or $t=(t_e+1)$. Factor Δt seems to be here grounded. As for the function

$$\frac{a_1}{t_s} \cdot \frac{(t_e+1-t)}{t}, \quad (5)$$

we leave it as a hypothesis satisfying the condition: the larger the age, the less $|\Delta M_1|$ is.

The increment ΔM_2 is positive. It also depends on the age t and time interval Δt , but compared to ΔM_1 , it is directly proportional to t and inversely proportional to the time interval left for the fish to live. Therefore it can be assumed that:

$$\Delta M_2 = a_2 \cdot \frac{t}{(t_e + 1 - t)} \cdot \Delta t, \quad (6)$$

where a_2 - proportionality coefficient, year⁻².

This function increases with increasing age t and interval Δt , it is zero at t or $\Delta t = 0$ and turns into $+$ at $t = (t_e + 1)$.

Thus, function $M(t)$ should satisfy the condition:

$$\Delta M = -a_1 \cdot \left(\frac{t_e + 1 - t}{t_s \cdot t} - k_1 \cdot \frac{t}{t_e + 1 - t} \right) \Delta t, \quad (7)$$

where $k_1 = \frac{a_2}{a_1}$, year⁻¹.

By dividing both parts of equation (7) by Δt and moving to the limit with $\Delta t \rightarrow 0$, we obtain the ordinary differential equation with separated variables:

$$\frac{dM(t)}{dt} = -a_1 \cdot \left(\frac{t_e + 1 - t}{t_s \cdot t} - k_1 \cdot \frac{t}{t_e + 1 - t} \right). \quad (8)$$

The solution of this equation is the function

$$M(t) = \frac{a_1}{t_s} \cdot \{ (1 - k_1 \cdot t_s) \cdot t - (t_e + 1) \cdot [\ln(t) + k_1 \cdot t_s \cdot \ln(t_e + 1 - t)] \} + b. \quad (9)$$

It represents the change of instantaneous coefficients of total natural mortality of cod in relation to age. In the interval $[t_r, t_e + 1)$, the function (9) is defined, continuous and has a single stationary point:

$$t = \frac{t_e + 1}{1 + \sqrt{k_1 \cdot t_s}}, \quad (10)$$

$\lim_{t \rightarrow t_e + 1} M(t) = \infty$. Let us assume that at $a_1 > 0$, $\min M(t) = M(t_s)$. In this case

$$k_1 = \frac{(t_e + 1 - t_s)^2}{t_s^3}. \quad (11)$$

Based on the hypothesis by Tyurin suggesting that natural mortality of fish is minimal at the age corresponding to the period of maturation (Tyurin, 1962, 1963, 1972), it can be assumed that parameter t_s expresses the age at which the number of mature fish of the generation under consideration reaches 50 % of their abundance. Thus, function $M(t)$ allows for a very important conceptual relationship between the natural mortality of cod and their age at maturity, theoretical maximum age and, as it will be shown later, length and weight growth. Its additive components derived on the basis of similar reasoning are accordingly as follows:

$$M_1(t) = \frac{a_1}{t_s} \cdot (t - (t_s + 1) \cdot \ln(t)) + c_1 \quad \text{and} \quad (12)$$

$$M_2(t) = a_2 \cdot (-t - (t_e + 1) \cdot \ln(t_e + 1 - t)) + c_2, \quad (13)$$

where c_1 and c_2 - integration constants, $c_1 + c_2 = b$. When $M_1(t_e + 1) = 0$ then

$$c_1 = -\frac{t_e + 1}{t_s} \cdot a_1 \cdot (1 - \ln(t_e + 1)). \quad (14)$$

For the sake of **briefness** the term "natural mortality coefficient" will further be used instead of definition "instantaneous natural mortality **coefficient**".

Algorithm of model parameters estimation.

Let's express a number of fish of a fixed generation at the age of t_r as a sum of two summands. The first augend is a cohort of fish which will die in the process of fishing, the addend is a cohort of fish which will die because of natural reasons only. We **beleave** that under intensive fishery there are no big numbers of fish older than t_λ in the area, where t_λ is the last age group in the commercial stock, $t_\lambda \ll (t_e + 1)$. Therefore, not a single fish in the second cohort will survive till the age of $(t_e + 1)$. Assuming further that natural mortality coefficient is species-related, historical, hereditary and, consequently, very conservative (Tyurin, 1972), i.e. it is basically unvariable at the same theoretical maximum age t_e , it can be stated that the situation will remain unchanged even in the absence of fishery. However, even in this case fish from the first cohort will also be dying from natural reasons only, and, consequently, some specimens just from this cohort will survive till the age of t_e

In the theory of dynamics of fish abundance, the function $N(t)$, the number of fish of the discussed generation at the time moment t is assumed to be considered continuous, therefore, let's think that a number of fish from the first cohort at the age of $(t_e + 1)$ in the absence of fishery will be less than 1. For definiteness, we assume that $N(t_e + 1) = 0,9$. Probably, the biological sense of the last equation is that a number of alive fish at the age of $(t_e + 1)$ is equal to 0.

$$\text{If } \frac{dN(t)}{dt} = -M(t) \cdot N(t), \quad \text{then} \quad (15)$$

$$N(t) = N(t_r) \cdot \exp \left\{ - \int_{t_r}^t M(t) dt \right\}. \quad (16)$$

In accordance with our assumption let's take the abundance of the discussed cohort at the age of t_r as equal to the abundance of the virtual population at this age, i.e.:

$$N(t_r) = \sum_{t=t_r}^{t_\lambda} C_t, \quad (17)$$

where C_t - a number of fish at the age oft caught **from** the year class
 which went through the fishery;
 t_λ - the age of the last age group in the commercial stock.

The expression (16) has two unknown parameters a_1 and b to be determined, which should be such that inequalities $N(t_e+1) < 1$, $a > 0$ and $\min M(t) > 0$ are satisfied. To estimate them, let's express the year class biomass at the age oft as:

$$P(t) = N(t) \cdot w(t), \quad (18)$$

where $w(t) = a_3 \cdot \ell_\infty^{b_1} \cdot \{1 - \exp(-k \cdot (t - t_0))\}^{b_1}$ - the equation characterizing the weight growth of fish;

ℓ_∞, k и t_0 - parameters of the Bertalanffy equation;

a_1 and b_1 - parameters of **allometric** growth.

Since there is the age t_c , at which the year class biomass has a maximum, one can write down that

$$P'(t) = 0. \quad (19)$$

Solving this equation relative to b , we find that

$$b = a_1 \cdot \left(\frac{t_e + 1}{t_s} \cdot \ln(t_c) + k_1 \cdot (t_e + 1) \cdot \ln(t_e + 1 - t_c) - t_c \cdot \frac{1 - k_1 \cdot t_s}{t_s} \right) + \frac{b_1 \cdot k}{\exp(k \cdot (t_c - t_0)) - 1}. \quad (20)$$

Let's denote the mean integral value of the natural mortality coefficient in the interval from t_e to (t_e+1) through $\bar{\mu}_{t_e}$.

$$\bar{\mu}_{t_e} = \int_{t_e}^{t_e+1} M(t) dt. \quad (21)$$

Since $\lim_{t \rightarrow t_e+1} M(t) = \infty$, then

$$\int_{t_e}^{t_e+1} M(t) dt = \lim_{\varepsilon \rightarrow 0} \int_{t_e}^{t_e+1-\varepsilon} M(t) dt. \quad (22)$$

Improper integral (21) converges, since

$$\lim_{\varepsilon \rightarrow 0} \int_{t_e}^{t_e+1-\varepsilon} M(t) dt \text{ exists and is equal to}$$

$$\left\{ a_1 \cdot (2t_e + 1) \cdot \frac{1 - k_1 \cdot t_s}{2t_s} + [t_e \cdot \ln(t_e) - (t_e + 1) \cdot \ln(t_e + 1) + 1] \cdot \frac{t_e + 1}{t_s} \right\} +$$

$$+ a_1 \cdot k_1 \cdot (t_e + 1) + b. \quad (23)$$

Thus, if

$$\bar{\mu}_{t_e} = \lim_{\varepsilon \rightarrow 0} \int_{t_e}^{t_e + 1 - \varepsilon} M(t) dt \quad \text{and} \quad (24)$$

$$N(t_e + 1) = N(t_e) \cdot \exp(-\bar{\mu}_{t_e}), \quad \text{then} \quad (25)$$

$$N(t_e) = N(t_e + 1) \cdot \exp\left(\lim_{\varepsilon \rightarrow 0} \int_{t_e}^{t_e + 1 - \varepsilon} M(t) dt\right). \quad (26)$$

On the other hand, it follows from the equality (16) that

$$N(t_e) = N(t_r) \cdot \exp(-a_1 \cdot (A + B) - (t_e - t_r) \cdot b), \quad (27)$$

$$\text{where } A = -\frac{1 - k_1 \cdot t_s}{2t_s} \cdot t_r^2 - \frac{t_e + 1}{t_s} \cdot (1 - \ln(t_r)) \cdot t_r + k_1 \cdot (t_e + 1) \cdot (t_e + 1 - t_r) \cdot (1 - \ln(t_e + 1 - t_r)), \quad (28)$$

$$B = \frac{1 - k_1 \cdot t_s}{2t_s} \cdot t_e^2 + \frac{t_e + 1}{t_s} \cdot (1 - \ln(t_e)) \cdot t_e - k_1 \cdot (t_e + 1). \quad (29)$$

By equating the right-hand parts of equalities (26) and (27), we obtain:

$$\ell n \frac{N(t_e + 1)}{N(t_r)} = a_1 \cdot f_1 - (t_e + 1 - t_r) \cdot b, \quad (30)$$

where

$$f_1 = -\frac{1 - k_1 \cdot t_s}{2t_s} \cdot ((t_e + 1)^2 - t_r^2) + \frac{t_e + 1}{t_s} \cdot ((1 - \ln(t_r)) \cdot t_r - (t_e + 1) \cdot (1 - \ln(t_e + 1))) -$$

$$- k_1 \cdot (t_e + 1) \cdot (t_e + 1 - t_r) \cdot (1 - \ln(t_e + 1 - t_r)). \quad (31)$$

Putting the expression (20) instead of b into equality (30), we obtain:

$$a_1 = \frac{f_3 + \ell n \frac{N(t_e + 1)}{N(t_r)}}{f_1 - f_2}, \quad (32)$$

$$\text{where } f_2 = (t_e + 1 - t_r) \cdot \left(\frac{t_e + 1}{t_s} \cdot \ln(t_c) + k_1 \cdot (t_e + 1) \cdot \ln(t_e + 1 - t_c) - \frac{1 - k_1 \cdot t_s}{t_s} \cdot t_c \right), \quad (33)$$

$$f_3 = \frac{(t_e + 1 - t_r) \cdot b_1 \cdot k}{\exp(k \cdot (t_c - t_0)) - 1}, \quad (34)$$

If age t_c is known, parameters a_1 and b can be found by formulae (32) and (20).

Scanning t_c with the accuracy to 0,1 in a big range of ages, for example, in the range from t_r to $(t_\lambda+2)$, we obtain different values of a_1 and b parameters. Let's assume unknown parameter t_c to be equal to a value at which a_1 and $\min M(t) > 0$, and the component $M_2(t)$, in the total natural mortality, caused by endogenous factors and parasites, is equal to zero at age $t=0$.

To evaluate t_e parameter, it is assumed that it corresponds to the length of the largest cod specimen (169 cm) known at present (Suvorov, 1948), the age of which was unfortunately not determined. The calculation of it was done in accordance with the back linear dependence between maximally possible theoretical duration of cod life under the real ecological conditions and a metabolism parameter k :

$$t_e = t_0 - \frac{1}{k} \cdot \ln \left(1 - \frac{\ell_{t_e}}{\ell_\infty} \right), \quad (35)$$

which follows from the Bertalanffy equation. Asymptotic length ℓ_∞ is determined as equal to 220 cm. It is assumed constant for all year classes.

Results and discussion.

Variability of t_s parameter has a dangerous tendency to decrease (Fig. 2). It agrees well with the tendency described earlier (Tretyak, 1984). Approximation of t_s parameter by a logic curve

$$\hat{t}_s = a_4 + \frac{a_5}{1 + \exp(a_6 \cdot G + a_7)}, \quad (36)$$

where G - a year of a population birth ($G = 1938, 1939, \dots, 1990$);

(a_4-a_7) - параметры, ($a_4=6.4, a_5=3.254, a_6=0.145, a_7 = -286.296$),

gives grounds to think that during 1938-1990 period it reduced by a value equal to the distance between asymptotes of this curve (a_5), a tendency to the diminishing of t_s parameter was the strongest one in year classes of the 1970's (bend point is $G_0 = -a_7/a_6 \approx 1974$), and the approximate limit, nearby which t_s parameter will be varying, will probably be the low asymptota (a_0). In accordance with the criterion of Polyakov (Lapin, 1971), diminishing oft, parameter by more than three years has led to the two times increase of speed of cod population reproduction.

Remainders $(\Delta t_s)_j = (t_s)_j - (\hat{t}_s)_j$ has a quasicyclic trend which can be well approximated by a sum of six harmonics:

$$(\Delta t_s)_j = A_0 + \sum_{i=1}^6 (A_i \cdot \sin(w_i \cdot j) + B_i \cdot \cos(w_i \cdot j)) , \quad (37)$$

where j - ordinal number of year class ($j=1, 2, 3, \dots, 45$);
 w_i - frequency of i harmonic ($w_1=0.328, w_2=0.580, w_3=0.749,$
 $w_4=0.908, w_5=1.433, w_6=3.023$);
 A_0, A_i, B_i - coefficients of the trend ($A_0=0.004, A_1=-0.081, A_2=0.064,$
 $A_3=0.009, A_4=0.114, A_5=-0.052, A_6=-0.087, B_1=-0.037,$
 $B_2=0.312, B_3=-0.110, B_4=-0.065, B_5=0.074, B_6=0.005$),

frequencies of fluctuations of which are close to harmonics frequencies specific for quasicyclic fluctuation of recruitment.

In accordance with equation (35) the change of parameters k and t_e is asynchronous (Fig. 3). Calculations show that growth rate and maximum possible lifespan of cod from year classes after 1975 changed sharply. Time series of these parameters can be divided into two periods: 1946-1975 and 1976-1990. Mean value and amplitude of fluctuation of k parameter in the second period is much larger. Theoretically maximum age diminished by approximately 3.5 years. In spite of its decrease, generative phase of life of cod increased by 20 %.

Such a change of parameters k and t_e taking place on the background of the other undesirable tendencies, namely: decrease of 50% maturity age and a portion of females in the spawning population and increase of a portion of mature fish among the same length cod (Ponomarenko and Yaragina, 1995; Ponomarenko et al., 1996), led to the change of parameters a_1 and b of function $M(t)$ and to a slight, by approximately 0.5 year, reduction of theoretical age t_c at which the year class biomass reaches its maximum in the absence of fishery.

It is generally assumed that the increase of the growth rate under the decrease of the life duration and mean age of mature fish causes the increase of the generation natural mortality (Lapin, 1971; Borisov, 1978b). Results of calculations of average integral values of natural mortality coefficients of 46 year classes of cod in each age from 3 to (t_e+1) years show that the idea on unchangeable natural mortality of cod during the fishery period of their life is very approximate (Fig. 4). Natural mortality coefficient varies not only with increasing age of fish but between year classes as well. It is practically independent of the year class strength. Parameters t_s and t_e have greater effect on its variability. Fig. 4 shows clearly the tendency towards decrease of this coefficient with time in younger age groups and its increase in older ones. We can identify two groups of year classes for the after the war period for which natural mortality coefficients are greatly different. These are 1946-1975 year classes and those after 1975. For the first group, the mean value of average integral coefficients

of natural mortality in the interval of 3-16 years is equal to 0.239, which is only 16% more than the magic value of 0.20 which has been used till now to assess the stock, to establish biological reference points and total allowable catch of cod. We are astonished by and delighted with the brilliant intuition of researchers proposed this value for the first time. However, for year classes of the second group this value is 10 % larger. In the first and second group it was 0.759 and 0.846 in the interval of $(3-(t_e+1))$ years and 1.285 and 1.670 in the interval of $(16-(t_e+1))$ years. It should be mentioned also that in cod there is a very high degree of differentiation of mortality in the life intervals of (3-16) and $(16-(t_e+1))$ years. In the first interval for the whole time series it is 5.4 times less than in the second. There is also differentiation of natural mortality in intervals $(3-t_s)$ and (t_s-16) years (Fig. 5). For the first group of year classes it is small: the mean coefficient in the second interval is 0.009 or 4% larger than that in the first one. For the second group the differentiation is much more significant (more than 11 times). The mean coefficient in the second interval is 0.092 or 46% larger than that in the first interval. Undesirable growth of differentiation occurred due to decreased natural mortality at ages younger than 9 years and increased mortality in older age groups (Fig.5b), which was due to a considerable change of its structure. In the second group the exogenous component decreased and endogenous increased (Fig.6).

The increase of cod growth rate and essentially changed structure of the natural mortality led to the change of the relative and absolute biomass of year classes in the big range of ages (Fig. 7). At $M=\text{const.}=0.20$ the mean relative biomasses of year classes in the second group much bigger than those in the first one for all fishable ages. In the first group the biomass index at $M=M(t)$ is less than at $M=0.20$, in the second group both indices are almost identical in the interval from 3 to 11 years while further on the first one drops rapidly compared to the second. These very important circumstances reveal a wrong existing optimistic conception of the size of biomass of year-classes in the first group and together with reduced age-at-maturity suggest a different in qualitative terms structure of the spawning population in the second group where younger fish began to prevail. The mean biomass of year-classes at all fishable ages is less in the second group than in the first (Fig. 7b). This is due to almost two times decline of the mean abundance of year-classes at age t_r .

The obtained results correspond well with a hypothesis on the presence of groups of early-, middle- and late-maturing fish in each year class of cod (the same as in the majority of other fish species). Due to this hypothesis (Borisov, 1978b), each group unites specimens with a certain specific genotype. Under the intensive fishery, the specimens of the last group have less chances to survive till the first and subsequent spawnings. The abundance of this group fish decreases as much that they do not participate in the reproduction. Their reproductional contribution is close to zero. The

reproductional contribution of early- and middle-maturing fish with less duration of life increases. These fishes have an advantage in formation of future year classes and in formation of the genofond of the spawning population. The supposed dividing of fish into early-, middle- and late-maturing specimens under conditions of a directed selection of intensive fishery had to cause in a time the increase of a portion of mature fishes among the same size cod that happened in-between the 1960's and 1970's (Ponomarenko and Yaragina, 1995). In the 1980's, this process increased.

Increased growth and production rate, longer generative period and a slight decrease of age t_c are still able in our view to support extremely intensive fishery for cod established historically, however, they can not probably ensure a high level of recruitment to **the** commercial stock observed in post-war years and correspondingly high levels of allowable catch.

The mean integral values of natural mortality coefficients of cod at the age of (3- 15) in different years of fishery are presented in Table. Outstanding values at the age 4- 15 in the left-hand part of the Table are estimated through a regressional equation

$$\hat{M}_{t,j} = a_{8,t} \cdot \omega_{t,j}^{a_{9,t}} \cdot \exp(a_{10,t} \cdot j + a_{11,t} \cdot \exp(a_{12,t} \cdot T_j + a_{13,t} \cdot \exp(a_{14,t} \cdot (\Delta t_s)_j))), (38)$$

where $a_{8,t}$ - $a_{14,t}$ - parameters of the equation, ($t=4,5,6, \dots, 15$);

$\omega_{t,j}$ - mean weight of cod from year-class j at age t , kg;

T_j - mean water temperature in the main branch of the Murman

Current in O-200 m in the first three years of life of year-class j ;

$(\Delta t_s)_j$ - deviations $(t_s - \hat{t}_s)_j$, approximated by the superposition of six harmonics (37).

Outstanding values of the natural mortality **coefficiens** for cod at age 3-8 in the **right-** hand part of the table are calculated by the following regression equation:

$$M_{t,j} = a_{15,t} \cdot \omega_{t,j}^{a_{16,t}} \cdot \exp(a_{17,t} \cdot j + a_{18,t} \cdot \exp(a_{19,t} \cdot T_j)), \quad (39)$$

where $a_{15,t}$ - $a_{19,t}$ - parameters of **the** equation, ($t = 3,4,5, \dots, 8$).

Parameters $a_{8,t}$ - $a_{14,t}$ and $a_{15,t}$ - $a_{19,t}$ are determined by the method of conjugate gradients **from** the corresponding conditions:

$$\sum_{j=1946}^{1975} (M_{t,j} - \hat{M}_{t,j})^2 \Rightarrow \min, \quad (40)$$

$$\sum_{j=1976}^{1991} (M_{t,j} - \hat{M}_{t,j})^2 \Rightarrow \min. \quad (41)$$

Natural mortality coefficients presented in Table can be used for estimation of total and spawning stocks, biological reference points and total allowable catch of cod. They show a declining trend in younger age groups. After 1991 the coefficients for ages 3-5 are much less than those used by the ICES Arctic Fisheries Working Group.

Conclusions.

A mathematical model of variation of natural mortality coefficients of cod with age increasing from 3 years and further is suggested. The model explicitly reflects a conceptual relationship between natural mortality of cod, maturity age and theoretically maximum age of fish, and implicitly - between natural mortality, linear and weight growth. Premises of the model are formulated and a method of estimating its parameters is suggested. Simplicity and community of prerequisites for a wide range of hydrobionts give the possibility to test the model in relation to other species.

The coefficients of natural mortality of cod of 1946-1991 year classes are calculated. Calculations show that the idea of **unvariable** natural mortality of cod during the period of its life when it is exploited by the fishery (aged 3-15) is very approximate. It leads to an inadequate reflection of variations of absolute and relative biomass of cod year-classes and in older age groups in particular. There is a very high degree of differentiation of natural mortality in the life intervals (3-16) and $(16-(t_e + 1))$. In the first interval, the mortality is 5.4 times less than in the second one. Two groups of year classes were identified in the post-war history of fishery for which natural mortality coefficients differ greatly. These are year classes of 1946-1975 and year classes after 1975. In the first group, the mean value of average integral coefficients in the interval (3-16) constitutes 0.239. In the second group, it is 10 % larger. Besides, in the second group, the differentiation of coefficients in the interval $(3-t_s)$ and (t_s-16) years is 11 times stronger. The increase of natural mortality of cod is caused by the increase of their growth rate, decrease of age at 50% maturity and maximum possible theoretical lifetime.

Such a change of conceptual parameters of cod populations caused a two-times increase of the reproduction rate and 20-% increase of the generative period. However, with the decrease of age at maturity, proportion of females in the spawning population and increase of the proportion of mature fish among the same length fish, it also led to an undesirable change of the spawning population structure. At a faster rate it now produces fish growing quicker, maturing earlier, but experiencing higher natural mortality which are apparently unable to keep the high level of recruitment of the commercial stock

which existed before and correspondingly high level of allowable catches,

The natural mortality coefficients presented in the paper can be used for assessing the stock, setting biological reference points and total allowable catch of cod. After 1991 coefficients for ages 3-5 are much less than those used by the ICES Arctic Fisheries Working Group.

REFERENCES

AJIAD,A., S.MEHL, K.KORSBREKKE, A.V.DOLGOV, V.A.KORZHEV, V.L.TRETYAK and N.A.YARAGINA. 1992. Trophic relations of Northeast Arctic cod and their growth in dependence on feeding. In: Investigations of relationships between fish populations in the Barents Sea. Selected papers. Murmansk, PINRO, p. SO-100 (in Russian).

ANON. 1989. Regulation of fishery for cod and capelin of the Barents Sea considering their trophic links. (Editors: Tretyak, V. L., V. A. Korzhev, N. G. Ushakov, and N. A. Yaragina. The Union Conference on Rational Exploitation of Biological Resources of the USSR Outer and Inland Seas. Theses. Moscow. P. 109-110 (in Russian).

ANON. 1996. Report of the multispecies Assessment Working Group. ICES CM 1996/Asses:3. 183 pp.

ANON. 1999. Oceanographic conditions of the Barents Sea and their influence on the survival and development of young Northeast Arctic cod. (Editors: Ozhigin, V.K., V.L.Tretyak, N.A.Yaragina, and V.A.Ivshin). Murmansk, PINRO, 88 p.(in Russian).

ANON. 2000. Report of the Arctic Fisheries Working Group. ICES CM 2000/ACFM:3. 3 12 pp.

BORISOV, V.M. 1978a. On the post-spawning exhaustion of the Arcto-Norwegian cod. Rybnoe khozyaistvo, No. 9, p. 15-17 (in Russian).

BORISOV, V.M. 1978b. The selectional influence of fishery on populational structure of long-cycle fish. Voprosy ikhtiologii. Vol. 18, No.6(113), p. 1 .O 10- 1 .O 19 (in Russian).

BORISOV, V.M. and M.I. SHATUNOVSKY. 1973. On the possibility of usage of tissue water fullness index for evaluation of natural mortality of the Barents Sea cod. Trudy VNIRO, vol. 93, p. 301-321 (in Russian).

DOLGOV,A.V., V.A.KORZHEV and V.L.TRETYAK. 1995. Cannibalism and its importance for formation of recruitment of Arcto-Norwegian Cod in the Barents Sea. Precision and relevance of pre-recruit studies for fishery managements related to fish stocks in the Barents Sea and adjacent waters. Proceedings of the Sixth IMR-PINRO Symposium, Bergen, 14-17 June, 1994. (Ed. A. Hylen). IMR, Norway. P. 121-128.

DOLGOV,A.V. 1997. Distribution, abundance, biomass and feeding of thorny skate, *Raja Radiata*, in the Barents Sea. ICES CM 1997/GG:04, 22 p.

DOLGOV, A.V. 1999. Feeding and trophic relations of the Barents Sea cod in

the 1980- 1990's. Murmansk, PINRO, 24 p. (in Russian).

DOLGOVA, N.V. and A.V. DOLGOV. 1997. Stock status and predation of long rough dab (*Hippoglossoides platessoides*) in the Barents and Norwegian Seas. ICES CM 1997/HH:05, 16 p.

JAKOBSEN, T. 1992. Biological reference points for Northeast Arctic cod and haddock. ICES J.mar.Sci., 49:155-166.

JORGENSEN, T. 1990. Long term changes in age at sexual maturity of Northeast Arctic cod (*Gadus morhua* L.). J.Cons.int.Explor.Mer. 1990. Vol.46. P.235-248.

KORZHEV, V.A. and V.L. TRETYAK. 1989. The effect of cannibalism on the strength of recruitment to commercial stock of Arcto-Norwegian cod. ICES Symp. on Multispecies Model. Paper No.37. 16 p.

KORZHEV, V.A. and V.L. TRETYAK. 1992. Influence of cannibalism on the abundance of recruitment of the commercial stock of the Arcto-Norwegian cod. In: Investigation of relationships between fish populations in the Barents Sea. Murmansk, PINRO, p. 238-248 (in Russian).

KORZHEV, V.A., V.L. TRETYAK and A.V. DOLGOV. 1996. Multispecies model of the commercial community of the Barents Sea. Murmansk, PINRO, p. 28-39 (in Russian).

LAPIN Yu. E. 1971. Natural laws of fish population dynamics in dependence on their lifetime. Moscow, Nauka, 176 p. (in Russian).

OZHIGIN, V.K., V.L. Tretyak, N.A. YARAGINA and V.A. IVSHIN. 1994. Dependence of the Barents Sea cod growth upon conditions of their feeding on capelin and water temperature. ICES CM. 1994/G:32. 17 p.

OZHIGIN, V.K., V.L. TRETYAK, N.A. YARAGINA and V.A. IVSHIN. 1995. Dependence of growth of Arcto-Norwegian cod *Gadus morhua morhua* on water temperature and conditions of feeding on capelin *Mallotus villosus villosus*. Voprosy ikhtiologii, vol. 35, No. 3, p. 334-342 (in Russian).

OZHIGIN, V.K., V.L. TRETYAK, N.A. YARAGINA and V.A. IVSHIN. 1996. Growth of Arcto-Norwegian cod. Murmansk, PINRO, 60 p. (in Russian).

PONOMARENKO, I.Ya., and N.A. YARAGINA. 1995. Maturation rates of the Lofoten-Barents Sea cod *Gadus morhua morhua* in 1940-1980's. Voprosy ikhtiologii, vol. 35, No. 2: 219-228 (in Russian).

PONOMARENKO, I.Ya. and N.A. YARAGINA. 1996. Feeding and food relations. Cod in the Barents Sea ecosystem. In: The Barents Sea cod: biological and fishery essay. Murmansk, PINRO, p. 56-104 (in Russian).

PONOMARENKO, I.Ya., N.A. YARAGINA and V.P. PONOMARENKO. Growth, fatness, fecundity and maturation. In: Cod of the Barents Sea: biological and fishery essay. Murmansk, PINRO, p. 105-140 (in Russian).

SWOROV, E.K. 1948. Bases of ichthyology. Leningrad, Sovetskaya nauka. 580 p. (in Russian).

TRETYAK, V.L. 1984. A method of estimating the natural mortality rates of fish

at different ages (exemplified by the **Arcto-Norwegian** cod stock). Proceedings of the **Soviet/Norwegian** Symposium on Reproduction and Recruitment of Arctic cod. IMR, Bergen, Norway. p. **238-271**.

TRETYAK, V.L., V.A. **KORZHEV** and N.A. **YARAGINA**. 1991. Trophic relation of the Barents Sea cod and their dynamics. ICES CM 1991/G: 22-23 pp.

TRETYAK, V.L., V.A. **KORZHEV**, A.V. **DOLGOV**. 1999. Experience of the use of the MSVPA method for modelling of the fishery community in the Barents Sea. In: Biology and regulation of fishery for demersal fish of the Barents Sea and North Atlantic. Selected papers of PINRO. Murmansk, PINRO. (in Russian).

TYURIN, P.V. 1962. A factor of fish natural mortality and its role in the fishery regulating. Voprosy ikhtiologii, vol. 2, No. **3(24):403-427** (in Russian).

TYURIN, P.V. 1963. Biological grounds for regulation of fishery in the inland waters. Moscow, Pitschhepromizdat, 120 p. (in Russian).

TYURIN, P. 1972. Normal curves of survival and rates of fish natural mortality as a theoretical basis of fishery regulation. **GosNIORH**, vol. 7 1: 7 1 - 127 (in Russian).

Table

Mean integral coefficients of natural mortality of cod at the age of 3-15 in
different years of fishery

Age, years	A year of fishery								
	1949	1950	1951	1952	1953	1954	1955	1956	1957
3	0, 411	0, 475	0, 475	0, 415	0, 387	0, 320	0, 299	0, 323	0, 391
4	0, 370	0, 346	0, 398	0, 399	0, 351	0, 328	0, 272	0,255	0, 275
5	0, 311	0, 304	0, 301	0, 344	0, 345	0, 305	0, 286	0, 239	0, 224
6	0, 281	0, 280	0, 272	0, 269	0, 305	0, 307	0, 272	0, 257	0, 216
7	0, 234	0, 232	0, 219	0, 225	0, 247	0, 279	0, 280	0, 249	0, 237
8	0, 236	0, 248	0, 226	0, 225	0, 234	0, 234	0, 261	0, 264	0, 234
9	0, 250	0, 237	0, 224	0, 218	0, 273	0, 264	0, 229	0, 253	0, 257
10	0, 212	0, 225	0, 220	0, 222	0, 225	0, 240	0, 226	0, 231	0, 252
11	0, 236	0, 236	0, 229	0, 253	0, 262	0, 260	0, 256	0, 241	0, 240
12	0, 246	0, 268	0, 252	0, 231	0, 276	0, 290	0, 289	0, 284	0, 270
13	0, 325	0, 317	0, 307	0, 301	0, 302	0, 307	0, 313	0, 313	0, 307
14	0, 340	0, 336	0, 329	0, 322	0, 319	0, 320	0, 326	0, 333	0, 335
15	0, 387	0, 385	0, 379	0, 371	0, 361	0, 357	0, 360	0, 370	0, 380
3-15	0, 295	0, 299	0, 295	0, 292	0, 299	0, 293	0, 282	0, 278	0, 278

Table (Continuation)

Age, years	A year of fishery								
	1958	1959	1960	1961	1962	1963	1964	1965	1966
3	0, 312	0, 362	0, 340	0, 351	0, 326	0, 293	0, 253	0, 267	0, 245
4	0,330	0, 265	0, 306	0,289	0, 298	0,277	0,250	0,216	0,229
5	0, 241	0, 288	0, 234	0, 268	0, 253	0, 281	0, 243	0, 220	0, 192
6	0, 203	0, 218	0, 259	0, 212	0, 243	0, 229	0, 235	0, 219	0, 200
7	0, 201	0, 190	0, 202	0, 241	0, 199	0, 227	0, 213	0, 217	0, 203
8	0, 225	0, 194	0, 184	0, 194	0, 232	0, 193	0, 220	0, 206	0, 207
9	0, 226	0, 221	0, 192	0, 183	0, 192	0, 231	0, 194	0, 221	0, 204
10	0, 258	0, 225	0, 223	0, 196	0, 188	0, 195	0, 238	0, 200	0, 229
11	0, 258	0, 266	0, 229	0, 231	0, 205	0, 198	0, 204	0, 252	0, 213
12	0, 256	0, 272	0, 282	0, 240	0, 245	0, 220	0, 214	0, 218	0, 273
13	0, 298	0, 278	0, 294	0, 306	0, 257	0, 266	0, 240	0, 235	0, 238
14	0, 331	0, 320	0, 308	0, 323	0, 338	0, 279	0, 293	0,266	0, 263
15	0, 385	0, 378	0, 364	0, 346	0, 361	0, 380	0, 309	0, 328	0, 299
3-15	0, 271	0, 267	0, 263	0, 260	0, 257	0, 250	0, 239	0, 236	0, 230

Table (continuation)

Age, years	A year of fishery								
	1967	1968	1969	1970	1971	1972	1973	1974	1975
3	0, 330	0, 223	0, 215	0, 235	0, 259	0, 251	0, 240	0, 253	0, 255
4	0, 211	0, 281	0, 192	0, 185	0, 202	0, 221	0, 216	0, 207	0, 217
5	0, 203	0, 188	0, 248	0, 172	0, 165	0, 179	0, 196	0, 192	0, 188
6	0, 175	0, 186	0, 173	0, 227	0, 159	0, 153	0, 165	0, 180	0, 177
7	0, 187	0, 168	0, 176	0, 166	0, 216	0, 153	0, 146	0, 156	0, 170
8	0, 194	0, 180	0, 162	0, 172	0, 164	0, 214	0, 153	0, 145	0, 153
9	0, 203	0, 191	0, 179	0, 163	0, 174	0, 167	0, 219	0, 158	0, 148
10	0, 209	0, 205	0, 193	0, 183	0, 169	0, 181	0, 175	0, 231	0, 168
11	0, 244	0, 220	0, 212	0, 201	0, 192	0, 180	0, 193	0, 188	0, 251
12	0, 231	0, 266	0, 237	0, 225	0, 213	0, 207	0, 195	0, 210	0, 206
13	0, 302	0, 255	0, 296	0, 260	0, 244	0, 231	0, 226	0, 216	0, 233
14	0, 264	0, 339	0, 286	0, 334	0, 290	0, 268	0, 254	0, 251	0, 241
15	0, 296	0, 296	0, 386	0, 324	0, 380	0, 327	0, 299	0, 283	0, 281
3-15	0, 235	0, 230	0, 227	0, 219	0, 217	0, 210	0, 206	0, 205	0, 207

Table (continuation)

Age. years	A year of fishery								
	1976	1977	1978	1979	1980	1981	1982	1983	1984
3	0, 222	0, 255	0, 241	0, 305	0, 257	0, 256	0, 276	0, 285	0, 156
4	0, 219	0, 192	0, 219	0, 208	0, 260	0, 221	0, 221	0, 238	0, 243
5	0, 194	0, 195	0, 173	0, 196	0, 189	0, 233	0, 202	0, 201	0, 216
6	0, 173	0, 180	0, 181	0, 162	0, 184	0, 179	0, 219	0, 194	0, 193
7	0, 169	0, 168	0, 174	0, 175	0, 158	0, 180	0, 178	0, 216	0, 196
a	0, 166	0, 167	0, 168	0, 175	0, 175	0, 160	0, 183	0, 185	0, 223
9	0, 156	0, 168	0, 170	0, 175	0, 181	0, 181	0, 167	0, 194	0, 198
10	0, 156	0, 162	0, 174	0, 179	0, 187	0, 194	0, 193	0, 180	0, 211
11	0, 182	0, 168	0, 174	0, 185	0, 193	0, 204	0, 213	0, 210	0, 198
12	0, 279	0, 202	0, 185	0, 189	0, 202	0, 212	0, 227	0, 238	0, 234
13	0, 229	0, 314	0, 227	0, 207	0, 210	0, 223	0, 236	0, 256	0, 270
14	0, 261	0, 258	0, 359	0, 259	0, 233	0, 236	0, 250	0, 266	0, 292
15	0, 273	0, 296	0, 292	0, 413	0, 296	0, 266	0, 267	0, 283	0, 303
3- 15	0, 206	0, 210	0, 211	0, 218	0, 210	0, 211	0, 218	0, 227	0, 226

Table (continuation)

Age, years	A year of fishery								
	1985	1986	1987	1988	1989	1990	1991	1992	1993
	0, 187	0, 203	0, 229	0, 241	0, 224	0, 220	0, 229	0, 186	0, 203
4	0, 137	0, 163	0, 177	0, 199	0, 210	0, 196	0, 191	0, 199	0, 164
5	0, 217	0, 126	0, 148	0, 162	0, 183	0, 193	0, 181	0, 176	0, 183
6	0, 206	0, 201	0, 122	0, 141	0, 156	0, 177	0, 188	0, 177	0, 170
7	0, 195	0, 208	0, 196	0, 122	0, 139	0, 158	0, 180	0, 193	0, 183
a	0, 207	0, 206	0, 220	0, 198	0, 127	0, 143	0, 166	0, 191	0, 208
9	0, 239	0, 228	0, 227	0, 242	0, 208	0, 137	0, 152	0, 180	0, 210
10	0, 219	0, 265	0, 258	0, 256	0, 274	0, 226	0, 151	0, 166	0, 201
11	0, 235	0, 248	0, 301	0, 299	0, 296	0, 317	0, 251	0, 169	0, 185
12	0, 222	0, 267	0, 285	0, 349	0, 350	0, 346	0, 372	0, 285	0, 193
13	0, 265	0, 252	0, 307	0, 330	0, 408	0, 414	0, 409	0, 441	0, 328
14	0, 308	0, 302	0, 289	0, 355	0, 385	0, 482	0, 493	0, 486	0, 526
15	0, 335	0, 355	0, 347	0, 333	0, 414	0, 452	0, 573	0, 589	0, 581
3- 15	0, 229	0, 233	0, 239	0, 248	0, 260	0, 266	0, 272	0, 265	0, 257

Table (the end)

Age, years	A year of fishery						
	1994	1995	1996	1997	1998	1999	2000
3	0, 247	0, 212	0, 211	0, 208	0, 205	0, 202	0, 198
4	0, 177	0, 213	0, 185	0, 179	0, 175	0, 173	0, 174
5	0, 151	0, 163	0, 192	0, 160	0, 153	0, 153	0, 153
6	0, 178	0, 147	0, 157	0, 182	0, 143	0, 144	0, 144
7	0, 172	0, 181	0, 150	0, 158	0, 181	0, 142	0, 142
a	0, 197	0, 183	0, 193	0, 159	0, 166	0, 187	0, 144
9	0, 232	0, 220	0, 201	0, 214	0, 175	0, 181	0, 200
10	0, 238	0, 266	0, 253	0, 227	0, 242	0, 197	0, 202
11	0, 229	0, 274	0, 310	0, 295	0, 262	0, 280	0, 225
12	0, 209	0, 264	0, 321	0, 366	0, 349	0, 305	0, 328
13	0, 221	0, 239	0, 306	0, 378	0, 436	0, 415	0, 358
14	0, 382	0, 255	0, 275	0, 358	0, 447	0, 521	0, 495
15	0, 631	0, 446	0, 295	0, 318	0, 419	0, 531	0, 626
3- 15	0, 251	0, 236	0, 235	0, 246	0, 258	0, 264	0, 261

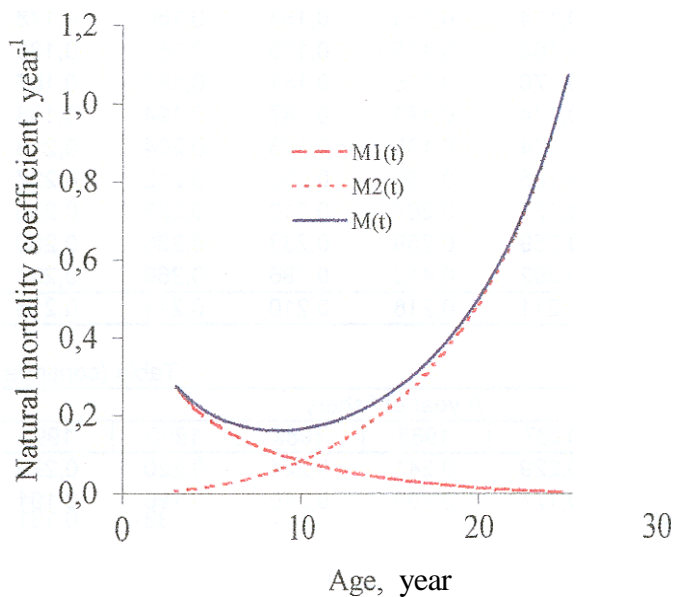


Fig. 1. General view of functions M , (t) , $M_2(t)$ and $M(i)$

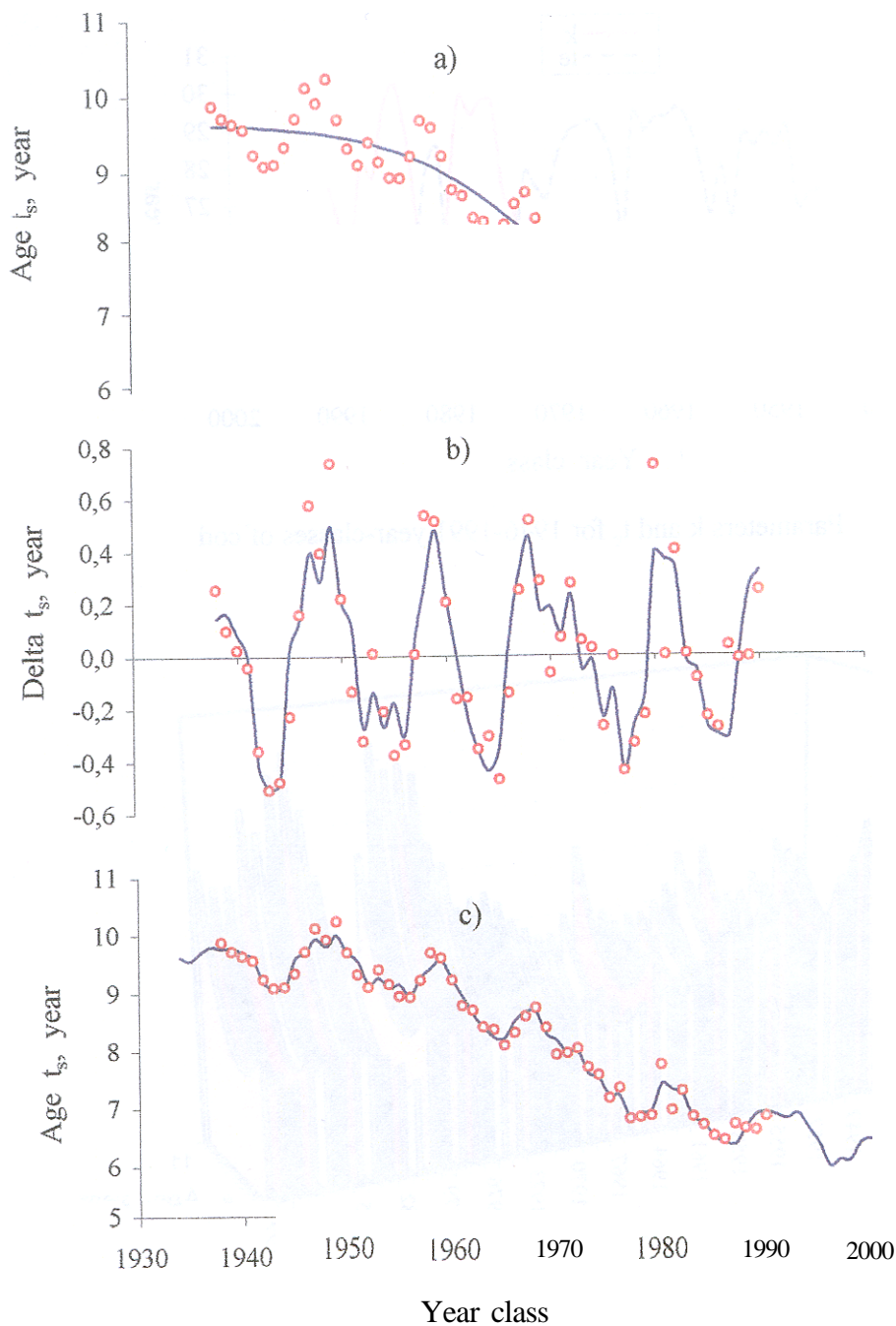


Fig. 2 Sequential approximation of age at 50% maturity (t_s) for various year-classes of cod a) approximation of t_s by logistic function; b) approximation of remainders by superposition of 6 harmonics; c) approximation of t_s by superposition of two trends: logistic and quasi-cyclic.

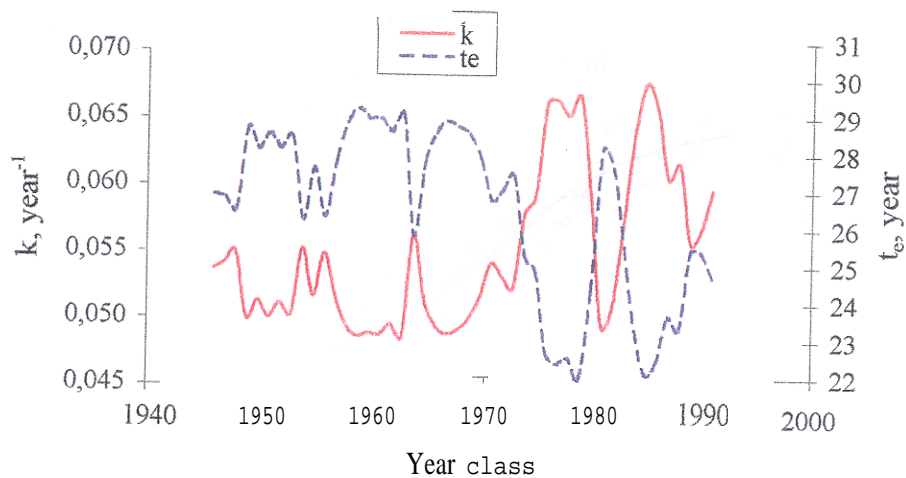


Fig. 3. Parameters k and t_e for 1946-1991 year-classes of cod

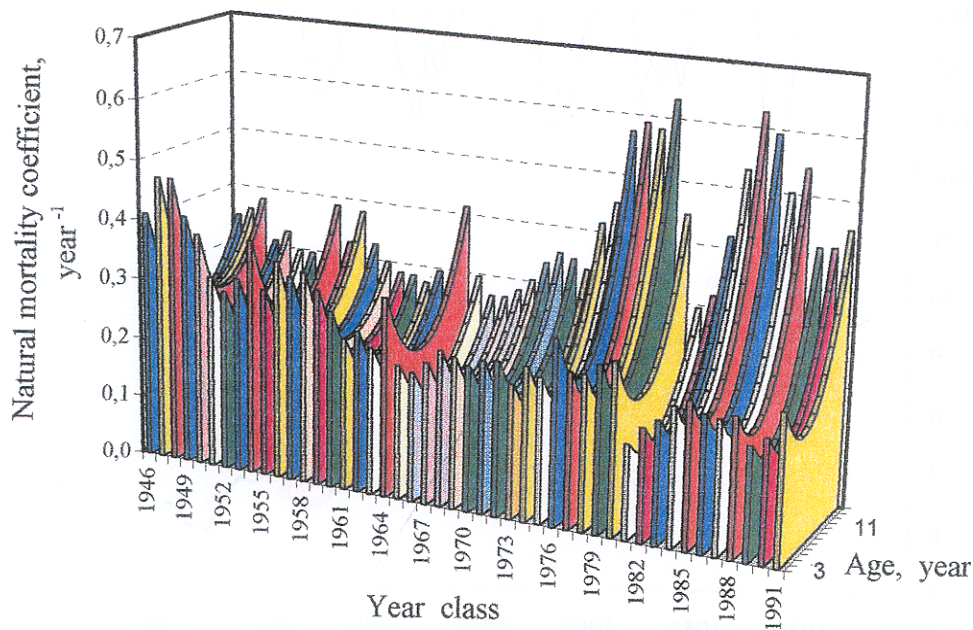


Fig. 4. Variation of the mean integral natural mortality coefficient 1946-1991 year-classes of cod with increasing age from 3 to 15

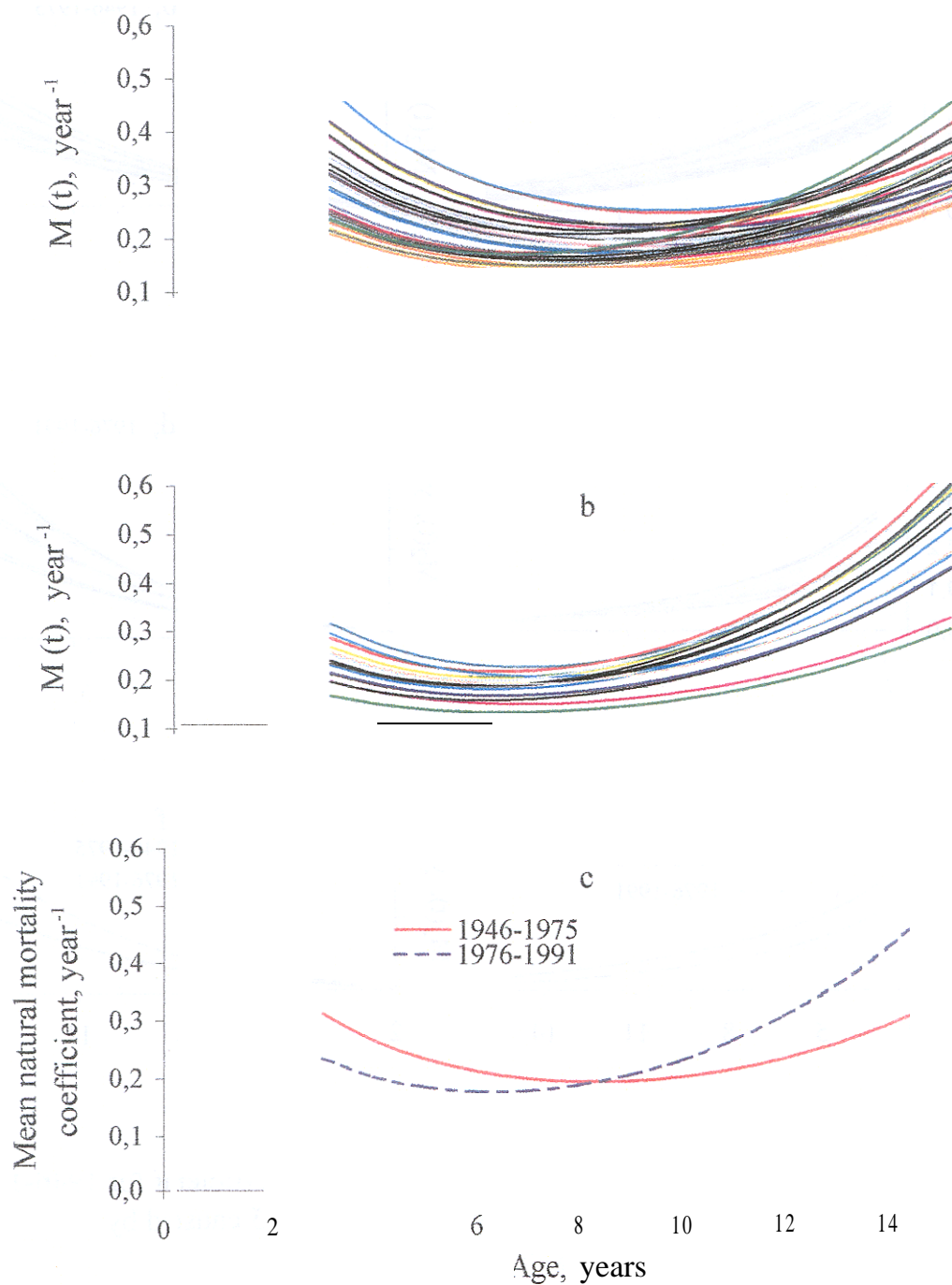


Fig. 5. Variation of the mean integral natural mortality coefficient for 1946-1991 year-classes of cod with increasing age from 3 to 15: a) 1946-1975 year-classes; b) 1976-1991 year-classes; c) arithmetic mean of mean integral values by age for 1946-1975 and 1976-1991 year-classes.

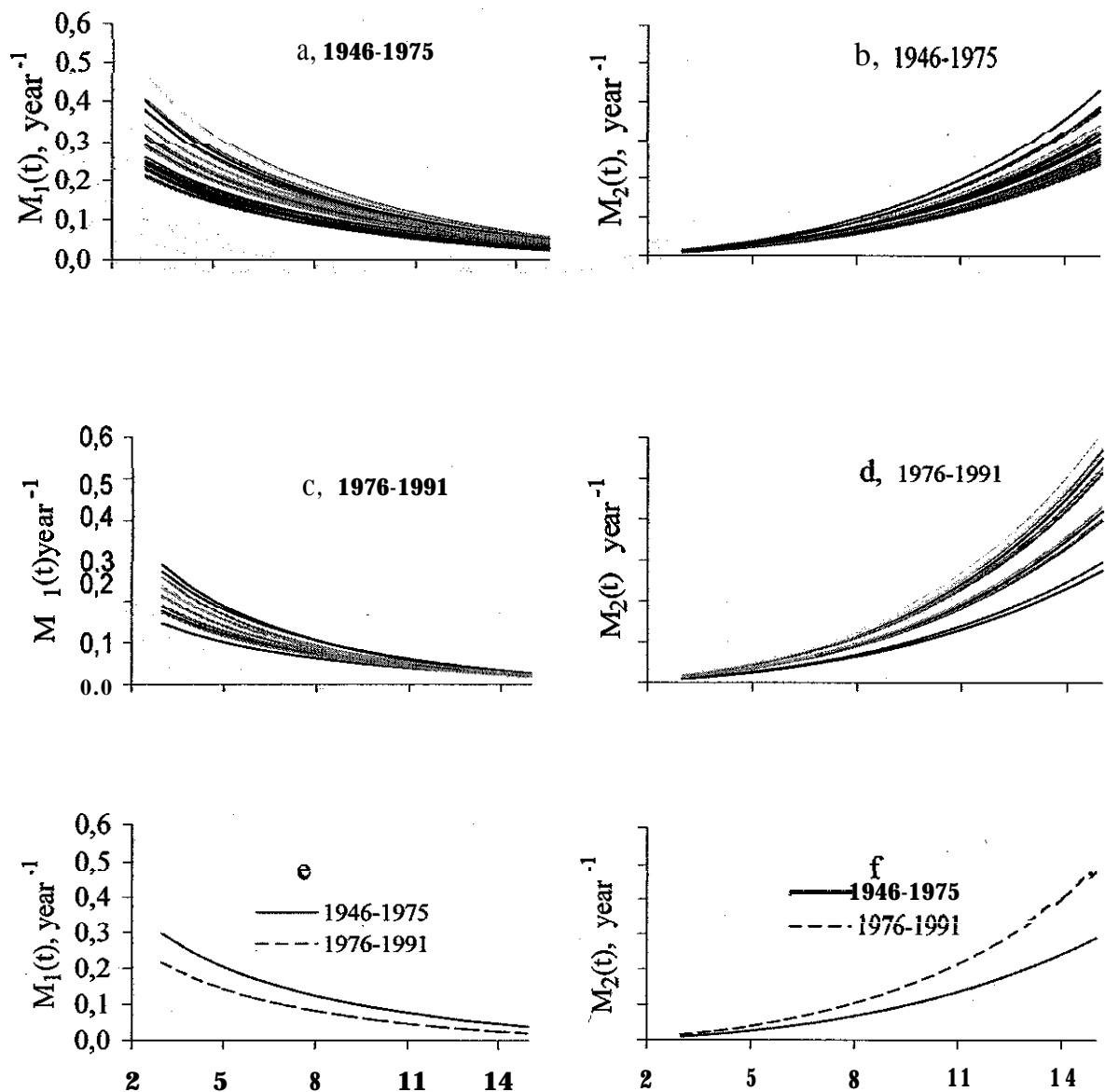


Fig. 6. Variation of the mean integral natural mortality coefficient for 1946-1 year-classes of cod with increasing age **from** 3 to 15 caused by exogenous (a,c,e) and endogenous (b, d, f) factors.

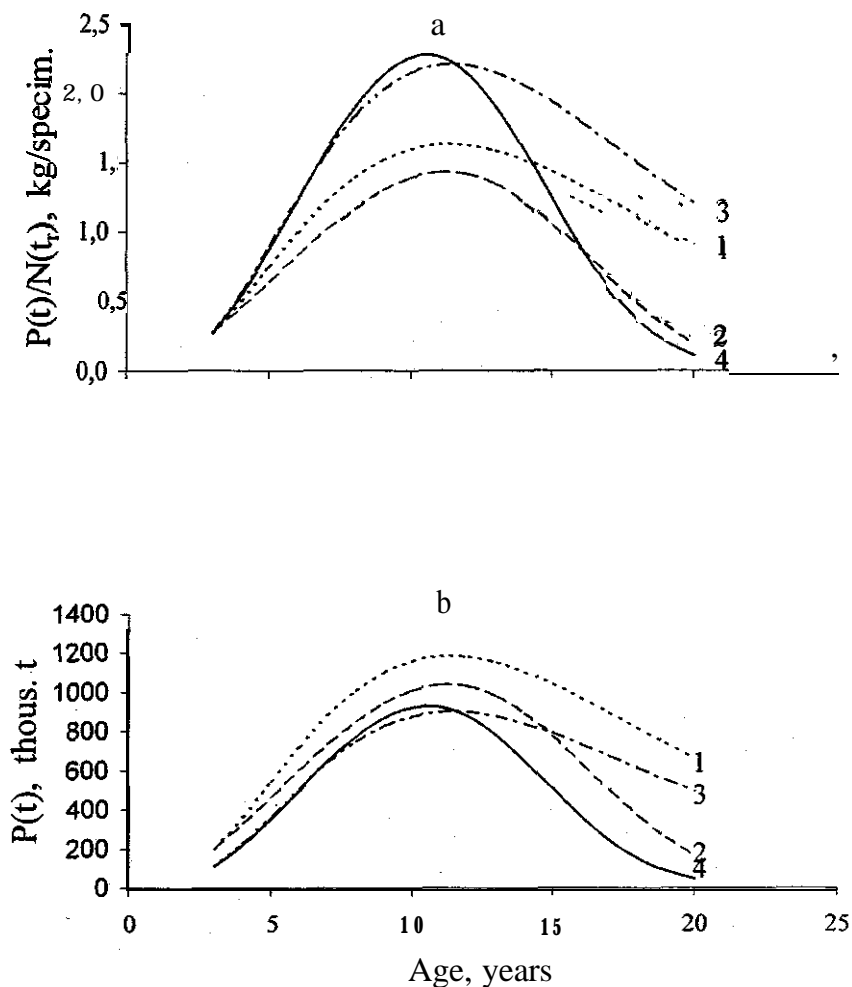


Fig. 7. Variation of the mean relative (a) and absolute (b) biomass of 1946-1975 and 1976-1991 year-classes of cod with increasing age from 3 to 20 at $M = \text{const} = 0.20$ and $M = M(t)$: (1) - $M = 0.20$, 1946-1975; (2) - $M = M(t)$, 1946-1975; (3) - $M = 0.20$, 1976-1991; (4) - $M = M(t)$, 1976-1991.